RELATIONSHIPS BETWEEN ANADROMOUS LAMPREYS AND THEIR HOST FISHES IN THE EASTERN BERING SEA

By

Kevin A. Siwicke

RECOMMENDED:

Dr. Trent Sutton

Mr. James Murphy

Dr. Andrew Seitz, Advisory Committee Chair

Dr. Shannon Atkinson
Chair, Graduate Program in Fisheries Division

APPROVED:

Dr. Michael Castellini
Dean, School of Fisheries and Ocean Sciences

Dr. John Eichelberger, Dean of the Graduate School

8/15/14
Date

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A

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Kevin A. Siwicke, B.S.

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Abstract

Arctic Lamprey *Lethenteron camtschaticum* and Pacific Lamprey *Entosphenus tridentatus* are ecologically and culturally important anadromous, parasitic species experiencing recent population declines in the North Pacific Ocean. However, a paucity of basic information on lampreys feeding in the ocean precludes an incorporation of the adult trophic phase into our understanding of lamprey population dynamics. The goal of this research was to provide insight into the marine life-history stage of Arctic and Pacific lampreys through lamprey-host interactions in the eastern Bering Sea. An analysis of two fishery-independent surveys conducted between 2002 and 2012 in the eastern Bering Sea revealed that Arctic Lampreys were captured in epipelagic waters of the inner and middle continental shelf and were associated with Pacific Herring *Clupea pallasii* and juvenile salmonids *Oncorhynchus* spp. In contrast, Pacific Lampreys were captured in benthic waters along the continental slope associated with bottom-oriented groundfish. Consistent with this analysis of fish assemblages, morphology of recently inflicted lamprey wounds observed on Pacific Cod *Gadus macrocephalus* was similar to morphology of Pacific Lamprey oral discs, but not that of Arctic Lamprey oral discs. Examination of 8,746 Pacific Cod, of which 4.9% had lamprey wounds, showed recent wounding rates positively increased with fish length up to 78 cm, and penetrating lamprey wounds were less likely to heal compared with superficial lamprey wounds, suggesting lamprey-related mortality. This study elucidates differences in the oceanic ecology between Arctic and Pacific lampreys and suggests a native lamprey can negatively impact hosts, which increases our understanding of lamprey ecology beyond traditional freshwater studies.

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General Introduction

Lampreys (Petromyzontiformes) are a resilient group of organisms that have persisted through extreme and cataclysmic mass extinction events. Along with hagfishes, lampreys comprise the only extant groups of jawless fishes, collectively referred to as agnathans, which are representatives of groups basal to all vertebrates (Hardisty and Potter 1971a). Modern adult lampreys are remarkably similar to the oldest fossilized lamprey dated at 360 million years before present, including the presence of an oral disc with circumoral teeth (Gess et al. 2006). This exceptional evolutionary longevity can be attributed to the unique and highly specialized life cycle exhibited by lampreys.

A simplified lamprey life cycle includes a larval phase, transitional period, and adult phase. All lampreys begin as microphagous filter-feeding larvae, living in riverine sediments for 3 to 7 years and recycling nutrients therein (Hardisty and Potter 1971b). Larval lampreys then undergo a metamorphosis that includes the development of functional eyes, a toothed oral disc, a toothed tongue, and externally exposed gill pores (Hardisty and Potter 1971a). Following metamorphosis, adult lampreys are classified as either nonparasitic or parasitic (Hardisty and Potter 1971a). Nonparasitic lampreys, also known as brook lampreys, forgo feeding as adults and remain relatively small, spawning and dying shortly after metamorphosis. In contrast, parasitic lampreys, collectively referring to lampreys that feed as adults on aquatic vertebrates via consumption of blood, flesh, or both, spend between a few months and several years feeding in freshwater or the ocean before traveling to headwater streams to spawn and die (Hardisty and Potter 1971a; Potter and Hilliard 1987). Paired species and stem-satellite species concepts are used to

describe nonparasitic lamprey species that likely derived from parasitic varieties, such that the larvae are indistinguishable, but the adult feeding habit and body size differ between life-history variants (Zanandrea 1959; Vladykov and Kott 1979). Because lamprey taxonomy continues to be a source of debate (Docker 2009), I will accept the taxonomy presented in Renaud (2011) for the purposes of this thesis.

Lampreys are commonly misperceived as a nuisance, which can mostly be attributed to the damaging impact of the invasive Sea Lamprey *Petromyzon marinus* on fish stocks in the Laurentian Great Lakes (Close et al. 2002). However, native lampreys are an integral component of the ecological systems in which they are found (Vladykov 1973; Renaud 1997). In contrast to the invasive Sea Lamprey, native lampreys play a valuable ecological role as prey at all stages of their lives: fishes consume eggs in redds, piscivorous birds and fishes feed on larvae from riverine sediments, marine mammals target concentrations of anadromous adults, and invertebrates eat the remains of post-spawning adults (Cochran 2009). Abundant anadromous lampreys may even buffer predation on other organisms such as salmonids (Close et al. 2002). Additionally, larval lampreys increase oxygen levels, maintain softness of the streambed and increase fine particulate organic matter found on the streambed of the freshwater ecosystems in which they are present (Shirakawa et al. 2013). Although there is still a paucity of research on the ecological services provided by lampreys, the known and potential benefits of intact native lamprey populations should not be overlooked.

As modern human societies continue to expand, lamprey habitats are at risk, and new challenges arise that lampreys must overcome (Renaud 1997). Chemical treatments

used to remove the invasive Sea Lamprey in the Great Lakes have additional adverse effects on native lamprey populations in the region (Schuldt and Goold 1980), and misguided poisoning of native lampreys has been carried out to rid ecosystems of these perceived pests (Close et al. 2004). Furthermore, poor water quality can negatively impact filter-feeding larvae (Myllynen et al. 1997), and in regions where water is diverted for agricultural irrigation, larval lampreys can become stranded in dewatered streambeds (Close et al. 2002). Additionally, exotic species can introduce a potential source of mortality to native lampreys that is often overlooked (Cochran 2009). One great challenge for lampreys is presented by the erection of waterway impediments; recently transformed lampreys that travel with water currents can become impinged on screens across water intakes of dams (Moursund et al. 2003) and adults can be impeded by these same barriers when traveling upstream to spawn (Beamish and Northcote 1989). Even when fish ladders are present, they are usually designed for strong swimming charismatic species and are inadequate for allowing unencumbered passage by comparatively weak swimming lampreys (Mesa et al. 2003; Keefer et al. 2013).

Cultures that exploit lampreys as a resource regard these species with esteem. Parasitic, anadromous lampreys grow much larger than brook lampreys, are energetically dense, and have predictable spawning runs, thus making them ideal targets for fisheries. Anadromous lampreys have a rich history as a regal food, enjoyed by Roman and English nobility, and although European River Lamprey *Lampetra fluviatilis* and Sea Lamprey continue to be targeted in fisheries across Europe today (Renaud 2011), their distributions are markedly reduced from historical accounts (Mateus et al. 2012). Indigenous cultures

often harvest lampreys for food and ceremonial uses, as is the case for the Maori of New Zealand who target the Pouched Lamprey *Geotria australis* (McDowall 1990) and native tribes in the U.S. Pacific Northwest who target the Pacific Lamprey *Entosphenus tridentatus* (Close et al. 2002). The Arctic Lamprey *Lethenteron camtschaticum* is similarly utilized as a subsistence resource in western Alaska, and this species is additionally targeted for commercial use in a centuries-old fishery in Japan and a developing fishery in Alaska (Renaud 2011).

The Arctic Lamprey and Pacific Lamprey inhabit the highly productive waters of the North Pacific Ocean during their adult trophic phase, and together are the only known species of lampreys found in the Bering Sea (Mecklenburg et al. 2002). Arctic Lampreys have a nearly circumpolar distribution in the northern hemisphere, inhabiting shallow nearshore waters from the Sea of Japan to the Bering Sea in the Pacific Ocean and the Beaufort Sea to the Barents Sea in the Arctic Ocean (Mecklenburg et al. 2002; Renaud 2011). Occurring at lower latitudes in the northern hemisphere, Pacific Lampreys occupy deeper waters and have a geographic distribution that extends from the Sea of Japan to the Bering Sea to the eastern North Pacific Ocean as far south as Mexico (Mecklenburg et al. 2002; Renaud 2011).

Arctic Lampreys are traditionally harvested by Alaska Natives from villages along the Yukon and Kuskokwim rivers using rakes and nets dipped through holes cut into river ice (Brown et al. 2005). Desired for human consumption and dog food because of their high lipid content, Arctic Lampreys remain an important resource in western Alaska (Brown et al. 2005; Andersen and Scott 2010). In 2003, a commercial fishery

began near Grayling, Alaska, and commercial harvest is limited to 20 metric tons because population information on this Arctic Lamprey stock is unknown (Bue et al. 2011). Additionally, traditional fishers for Arctic Lamprey in Japan use nets and baskets placed on the streambed that create breaks in the current to capture adults swimming upstream, later being sold as food and medicine (Honma 1960; Renaud 2011).

Population trends for Arctic Lamprey are poorly understood because of a lack of information, but harvest records may provide an indication of regional abundance trends. The International Union for Conservation of Nature Red List reports the status of Arctic Lamprey as "least concern," but it is acknowledged that population trends are unknown (Freyhof and Kottelat 2008). In Alaska, stake-holders recognize that Arctic Lamprey abundance and distribution remain poorly understood (ADFG 2006), but harvest records have been kept since 2003, when a commercial fishery began for this species. However, effort in this fishery is highly variable from year to year, so there is no reliable index of abundance in the region. Japanese harvest records are believed to track Arctic Lamprey abundance in that region, and catches of Arctic Lamprey declined nearly 90% from 1990 to 1997 in the Ishikari River which was largely attributed to overfishing (Yazawa 1998). Additional causes for this decline are likely acting in concert with overfishing, including stream channelization (Nagayama et al. 2008) and the construction of dams (Fukushima et al. 2007).

Although Pacific Lampreys are also found in rivers of Alaska and Japan (Renaud 2011), fisheries for Pacific Lampreys are primarily in the U.S. Pacific Northwest (Close et al. 2002). Native tribes of the Pacific Northwest catch Pacific Lampreys for food and

medicinal and ceremonial use, with traditional fishing grounds for numerous tribes on the main stem and tributaries of the Columbia and Klamath rivers (Close et al. 2002; Petersen 2009). Fishing for Pacific Lamprey is conducted using hooks, nets, and traps, and this tradition is deeply intertwined with many Pacific Northwest cultures, such that reductions in or extirpations of Pacific Lamprey populations can result in a loss of culture to these people (Close et al. 2002; Petersen 2009).

Pacific Lamprey populations in the U.S. Pacific Northwest have declined in recent decades, prompting local, state, and federal intervention (Luzier et al. 2011). For example, the average count of adult Pacific Lampreys passing Bonneville Dam on the Columbia River from 1997 to present was one-third that from 1939 to 1969 (Murauskas et al. 2013). A failed attempt to list the Pacific Lamprey under the Endangered Species Act in 2004, attributed to a lack of information on population trends, ultimately resulted in a bolstered effort to conserve and restore this species, including a multi-agency and multi-tribal conservation initiative drafted by the U.S. Fish and Wildlife Service (Luzier et al. 2011). Conservation actions to date include the translocation of adult Pacific Lamprey into headwater streams beyond dams (Ward et al. 2012) and the retrofitting of fish ladders to be more easily passable by lampreys (Moser et al. 2011). The complete successes of these projects remain to be seen, but the efforts themselves highlight improvements in the way resource managers view native lampreys in the USA.

Although the freshwater phases of Arctic and Pacific lampreys are being investigated for potential threats to these species, the adult trophic phase remains relatively unexplored, ignoring potentially important lamprey-host interactions. Because

Arctic Lampreys, Pacific Lampreys, and fishes bearing lamprey wounds are captured during fishery surveys conducted in the eastern Bering Sea, it is possible to investigate the adult trophic phase of lampreys in this region. The eastern Bering Sea is a highly productive ecosystem that is economically valuable because of the commercial fish resources present. These fish resources are ecologically valuable for the endemic Arctic and Pacific lampreys that feed therein. Thus, the eastern Bering Sea provides an ideal system for initiating studies on anadromous Arctic and Pacific lampreys and their hosts in the ocean, as well as elucidating important differences between lamprey species and their relationships with marine hosts.

The goal of this thesis is to investigate ecological interactions between anadromous lampreys and their marine hosts. My intention is to provide insight into the adult trophic phase of native lampreys, and inform future lamprey conservation and management programs. The studies in this thesis focus on Arctic and Pacific lampreys captured in the eastern Bering Sea and have been separated into two chapters with the following goals and objectives.

Chapter 1—Explore associations between the distributions of lampreys and potential hosts in the eastern Bering Sea:

- Compile vertical and horizontal distributions for anadromous lampreys in the eastern Bering Sea.
- Examine whether fish assemblages in regions with and without lampreys differ from one another.

- Explore associations between catches of potential host fishes and lampreys in fishery-independent surveys.

Chapter 2—Examine parasitic interactions between anadromous lampreys and Pacific Cod in the eastern Bering Sea:

- Discern which lamprey species inflicted wounds observed on Pacific Cod.
- Investigate the potential relationship between lamprey wounding rates and Pacific Cod length.
- Infer Pacific Cod survival via examination of lamprey wound severity and location on Pacific Cod across sequential stages of wound healing.

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Chapter 1:

Associations between anadromous lamprey distributions and potential host fishes in the eastern Bering Sea[1]

1.1 Abstract

Arctic Lamprey *Lethenteron camtschaticum* and Pacific Lamprey *Entosphenus tridentatus* are ecologically and culturally valuable native species that co-occur in the eastern Bering Sea. There is a paucity of information on anadromous lampreys feeding in the ocean; however, fish assemblages associated with lamprey distributions can be used to provide insight into potential lamprey-host interactions and foraging behavior of lamprey in the ocean. To examine lamprey distributions and potential hosts affecting those distributions, I utilized data from two fishery-independent surveys conducted between 2002 and 2012 in the eastern Bering Sea. I found that Arctic Lampreys predominantly inhabited waters of less than 100-m depth in northern regions on the inner and middle continental shelf in which Pacific Herring *Clupea pallasii* and juvenile salmonids *Oncorhynchus* spp. were common. Pacific Lampreys predominantly inhabited benthic waters deeper than 150 m along the continental slope and co-occurred with bottom-oriented fishes, including Greenland Halibut *Reinhardtius hippoglossoides* and Pacific Cod *Gadus macrocephalus*. Arctic and Pacific lampreys do not appear to have overlapping distributional ranges in the eastern Bering Sea, and as a result, these species likely interact with different fish assemblages. These results could be explained by differences in feeding strategies or host preferences by Arctic and Pacific lampreys.

[1]Siwicke, K. A. 2014. Associations between anadromous lamprey distributions and potential host fishes in the eastern Bering Sea. Prepared for submission to Transactions of the American Fisheries Society.

Alternatively, Arctic and Pacific lampreys may distribute differently, placing them in regions with different fish assemblages. Regardless, in the eastern Bering Sea, Arctic Lampreys are likely to impact Pacific Herring and juvenile salmonids, whereas Pacific Lampreys are likely to impact groundfish. This study provides an initial baseline of the oceanic ecology of lampreys, which increases our understanding of species-specific differences beyond traditional freshwater studies.

1.2 Introduction

Anadromous lampreys (Petromyzontiformes) are jawless fishes that play important ecological roles in freshwater and marine environments and are valuable to the cultures that harvest them (Renaud 2011). They are prey for a variety of fishes, birds, terrestrial and marine mammals, and invertebrates during their life cycle (Cochran 2009), and adults feed on aquatic vertebrates via consumption of blood, flesh, or both during their trophic phase (Potter and Hilliard 1987). Species of lamprey that feed as adults are referred to as parasites, whereas those that forgo feeding as adults are nonparasitic and generically referred to as brook lampreys (Hardisty and Potter 1971). Although lamprey fisheries occur in freshwater rivers, the parasitic species that feed in the ocean are the varieties targeted because of their large size, high caloric content, and predictable spawning runs. Anadromous lampreys are historically a regal food enjoyed by Roman and English nobility, and fisheries for European River Lamprey *Lampetra fluviatilis* and Sea Lamprey *Petromyzon marinus* continue across Europe today (Renaud 2011). In the USA, Alaska Natives living on the lower Yukon and Kuskokwim rivers target Arctic Lamprey *Lethenteron camtschaticum* in late November to early December using dip nets swept through holes cut in the frozen surface of the river (Brown et al. 2005), and native tribes in the U.S. Pacific Northwest fish for Pacific Lamprey *Entosphenus tridentatus* in the summer using nets, poles with hooks, and bare hands (Close et al. 2002).

Adult lamprey trophic ecology can be gleaned from evidence of lamprey-host interactions, including lampreys still attached to hosts and wounds left as a result of these encounters. Although lampreys are occasionally observed attached to large bodied

vertebrates such as whales (Pike 1951; Nichols and Tscherter 2011; Samarra et al. 2012) and sharks (Gallant et al. 2006), teleosts more frequently exhibit evidence of parasitic lamprey interactions, specifically wounds in their skin and muscle. These wounds have been observed on the following groups of teleosts in the North Pacific Ocean: Gadidae, Clupeidae, Salmonidae, Sebastidae, and Pleuronectidae (Sviridov et al. 2007; Orlov et al. 2009; Shevlyakov and Parensky 2010). Conversely, lamprey wounds are apparently absent on teleosts that possess protective body structures, slender body forms, slimy skin, or watery flesh such as members of Cottidae, Psychrolutidae, Hemitripteridae, Agonidae, Zoarcidae, Stichaeidae, Liparidae, and Macrouridae (Orlov et al. 2009).

Additional information about the trophic ecology of adult anadromous lampreys can be inferred from specimens opportunistically captured in the ocean. Lamprey captures in the Atlantic Ocean provide evidence that first-year Sea Lampreys feed on small fish in benthic waters of the continental shelf, whereas older Sea Lampreys feed on large pelagic species near the continental slope (Halliday 1991). Long-term data on Arctic Lamprey captures in the North Pacific Ocean (total-length range, 15–79 cm) suggests the greatest abundance occurs in the western Bering Sea in the upper 100 m of the water column (Orlov et al. 2014). Similarly, Pacific Lamprey captures in the North Pacific Ocean (total-length range, 12–85 cm) are most abundant in the Bering Sea, but are located in deeper waters and throughout the water column (Orlov et al. 2008).

Understanding the trophic ecology of adult lampreys in the ocean is important because hosts may experience adverse impacts from parasitic interactions with lampreys. For example, in the Fraser River plume, British Columbia, the flesh-feeding Western

River Lamprey *Lampetra ayersii* was estimated to consume hundreds of millions juvenile salmonids *Oncorhynchus* spp. and Pacific Herring *Clupea pallasii* (Beamish and Neville 1995). In the Amur River Estuary, Russia, the greatest source of early stage mortality for Chum Salmon *Oncorhyncus keta* and Pink Salmon *O. gorbuscha* smolts was attributed to feeding by Arctic Lamprey (Novomodnyy and Belyaev 2002). For the invasive Sea Lamprey in the Laurentian Great Lakes, lamprey parasitism reduced populations of native species such as Burbot *Lota lota* and Lake Trout *Salvelinus namaycush* and negatively impacted the rehabilitation of the imperiled Lake Sturgeon *Acipenser fulvescens* (Sutton et al. 2004; Stapanian et al. 2006). The potential severe consequences of lamprey-host interactions for host populations cannot be overstated.

An increased understanding of lamprey-host interactions has been identified as a research need for native lamprey species in the North Pacific Ocean (Mesa and Copeland 2009). However, the vast geographic area over which anadromous lampreys feed and the difficulty in capturing them makes this an arduous task. Although general distributions have been established for Arctic and Pacific lampreys by combining multiple years and data sources in the North Pacific Ocean (Orlov et al. 2008, 2014), details pertaining to interannual variation or mechanistic drivers are precluded in this approach. As a result, we still do not know if specific habitats are consistently being utilized by lampreys or why certain areas may be more important for one species or another. Furthermore, single-species distributions of Arctic and Pacific lampreys in the North Pacific Ocean show an apparent segregation of habitat use in the eastern Bering Sea, but to date, this phenomenon has not been explored, obviating underlying differences in how these

species distribute. Because we know that the adult phase of anadromous lampreys is characterized by feeding, one potential driver of the distributions of Arctic and Pacific lampreys in the eastern Bering Sea is the availability of hosts.

The goal of this study was to explore associations between the distributions of lampreys and potential hosts in the eastern Bering Sea. To accomplish this, I first compiled information on the vertical and horizontal distributions of Arctic and Pacific lampreys captured in the eastern Bering Sea. Once I established where Arctic and Pacific lampreys were found in this region, I examined whether fish assemblages in regions with and without lampreys differed from one another. Finally, I explored associations between catches of potential host fishes and lampreys in fishery-independent surveys. Addressing these objectives provides an initial step towards understanding the ecology of adult trophic-phase anadromous lampreys in the eastern Bering Sea.

1.3 Methods

I analyzed lamprey and fish catch data from two fishery-independent surveys occurring in the eastern Bering Sea. One survey was conducted in epipelagic waters and the other in benthic waters, and when combined, these surveys provided vertical and horizontal coverage of the region. To analyze the distributions of Arctic and Pacific lampreys in the eastern Bering Sea, I first summarized annual lamprey distributions by geographic region (horizontal) and survey (vertical). I then examined differences in fish assemblages in regions with and without lampreys using nonparametric analyses. Finally, I explored which potential hosts were most likely important to lampreys by examining correlations between lamprey CPUE and potential host CPUE.

1.3.1 Data sources, compilation, and processing

Catch rates of lampreys and surface-oriented teleosts were acquired from an epipelagic rope trawl survey conducted by the National Marine Fisheries Service (NMFS) as part of the Bering Aleutian Salmon International Survey (BASIS). This survey in eastern Bering Sea occurred annually from mid-August to early October of 2002 through 2012, but in 2008, effort was reduced because of a transition in survey programs, so this year was excluded from the analysis (Farley et al. 2009). Prior to 2008, the entire survey was conducted on one vessel, but following 2008, this survey was carried out concurrently in the northern and southern (south of 60° N) portions of the eastern Bering Sea using two vessels. Epipelagic survey gear consisted of a 198-m midwater rope trawl, modified for use in the epipelagic zone, with a 1.2-cm cod end mesh liner, and tows were 30 min in duration (Farley et al. 2009). Twenty-six stations sampled during one leg of the 2002 BASIS survey did not identify the species of captured lampreys. Because all other years of this survey only documented Arctic Lamprey in these regions, I assumed unidentified lampreys were the same species rather than remove these stations from the analysis.

Catch rates of lampreys and bottom-oriented teleosts were obtained from a benthic rope trawl survey conducted by the NMFS Resource Assessment and Conservation Engineering Groundfish Assessment Program. This survey occurred annually between June and August on the Bering Shelf from 1982 to 2013 and biennially along the Bering Slope from 2002 to 2012; however, the Bering Slope survey was not conducted in 2006 due to a lack of funding (Hoff 2013; Lauth and Nichol 2013). Because

lamprey captures were predominantly along the continental slope, analyses were limited to years with both a Bering Shelf and Bering Slope survey (2002, 2004, 2008, 2010, and 2012). Survey gear consisted of an 83-112 eastern otter trawl with a 25.3-m headrope, 34.1-m footrope, 8.9- to 10.2-cm mesh net, and 3.2-cm cod end mesh liner (Hoff 2013; Lauth and Nichol 2013). One leg during the 2010 Bering Slope survey did not identify the species of captured lampreys; however, based on the fact that all other lampreys captured by this survey were identified as Pacific Lamprey, I assumed that those unidentified lamprey were the same species rather than removing those stations from the analysis.

Catch data of teleosts and lampreys from each survey were summarized by Bering Sea Integrated Ecosystem Research Program (BSIERP) regions. There were 16 BSIERP regions (Figure 1.1), which divided the eastern Bering Sea along known oceanographic, bathymetric, and ecological boundaries (Ortiz et al. 2012). For example, the eastern Bering Sea was separated into three depth domains of 0–50, 51–100, and 101–150 m (Coachman 1986), and the boundaries of BSIERP regions often coincided with these domains. Any stations located outside of the BSIERP region boundaries were not examined further in this study. All survey-year-region combinations were included for compiling lamprey distributions, but a minimum of three stations sampled per year-region-combination was required for subsequent analyses to avoid inadequate characterization of fish assemblages in under-sampled regions (Tables 1.1 and 1.2).

For stations included in the analysis, CPUE by species was standardized to mass per unit of area swept by the trawl (kg/ha), and rare species were removed. Mass data

(kg) from the epipelagic trawl was converted to CPUE through division by the average area swept per unit time of 25 hectares per 30 min tow (Murphy et al. 2009). Rare species, defined as those occurring at less than 5% of stations within the study area for all years of a survey, were removed prior to analysis because they were unlikely to influence lamprey distribution, but would tend to distort clustering patterns that might exist in their absence. For the epipelagic trawl survey, the five species of Pacific salmon were further divided into a juvenile group, individuals in their first summer in the ocean and that generally do not exceed 300 mm in length, and an immature/mature group, which consisted of individuals that had already overwintered once in the ocean. I summarized the remaining teleost CPUE data for each survey-year-region combination by calculating the mean CPUE by teleost fish group. A total of 1,345 epipelagic stations and 2,946 benthic stations were examined for this analysis.

Because the primary interest of this study was the relationship between the presence of lampreys and their potential hosts, each survey-year-region combination was categorized as “High” or “Low” lamprey catch, defined below, and this factor was used for statistically testing whether fish assemblages differed in areas with and without lampreys. Because Pacific Lampreys were infrequently captured in the epipelagic survey (< 0.1% of stations), I limited my analysis of epipelagic teleost CPUE data to Arctic Lamprey. Arctic Lampreys were never captured at a benthic station, so I limited my analysis of benthic teleost CPUE data to Pacific Lamprey. The criterion for establishing High and Low lamprey catch categories varied slightly between surveys because the larger mesh size of the benthic trawl was believed to be less efficient at sampling lamprey

compared to the smaller mesh of the epipelagic trawl; in the epipelagic survey, the High lamprey catch category was defined as two or more Arctic Lampreys per year-region combination, whereas in the benthic survey, the High lamprey catch category was defined as one or more Pacific Lamprey per year-region combination.

1.3.2 Ordination analysis

To investigate whether fish assemblages in regions with High and Low lamprey catch differed from one another, I employed nonparametric multivariate analyses in the program PRIMER version 6.1.15 (Clarke & Gorley 2006). Summarized teleost CPUE data was compared to identify fish assemblages, such that year-region combinations with similar teleost groups occurring at similar proportions had similar fish assemblages. Because lamprey species were segregated by survey, data from the epipelagic survey and benthic survey were treated separately in the analysis. The resulting epipelagic survey matrix was 121 year-region combinations by 25 teleost groups, and the benthic survey matrix was 68 year-region combinations by 64 teleost groups. A two-part analysis was conducted for each survey to visualize and test for differences in fish assemblages between regions with High and Low lamprey catch.

First, I visualized patterns in fish assemblages among year-region combinations using nonmetric multidimensional scaling (NMDS), a nonparametric method that reduces similarities to rank order. To do this, I applied a square-root transformation to the summarized teleost CPUE data, deemphasizing high CPUE values, but not over-emphasizing low CPUE values. A similarity matrix was then constructed from the square-root-transformed data for each survey using a Bray-Curtis dissimilarity measure

(Clarke and Gorley 2006). An NMDS plot was then created for each survey based on rank orders from the similarity matrix, and multidimensional data was reduced to two or three dimensions. The Kruskal's stress value was used to estimate how well the NMDS scaling represented the multivariate data, such that values closer to zero provide a better representation of the data (Kruskal 1964). For this study, I only considered the three-dimensional solution if the Kruskal's stress value for the resulting NMDS in two dimensions was greater than 0.2, indicating a poor fit (Kruskal 1964).

Second, I used an analysis of similarity (ANOSIM) routine to test for significant differences in fish assemblages by lamprey catch group (High or Low). The ANOSIM test is a rank-based analog to an analysis of variance (ANOVA) test, establishing a permutation-based null distribution from the similarity matrix by which a test statistic R is compared (Clarke and Gorely 2006). I ran 9,999 permutations of the data for each survey to create a null distribution, and used R values to aid in interpreting group similarities, where an R value of zero indicated similarities between and within groups were equivalent and an R value of one indicated all year-region combinations within a group were more similar to each other than year-region combinations from the other group (Clarke and Gorely 2006). Additionally, an index of multivariate dispersion (MVDISP) was used to assess differences in variability between groups (Clarke and Gorely 2006). Significant differences between High and Low lamprey catch groups from an ANOSIM test ($\alpha = 0.05$) were interpreted using a similarity percentage (SIMPER) routine, which partitioned the contributions of individual teleost groups to the dissimilarity between year-region combinations with High and Low lamprey catch.

1.3.3 Lamprey and host correlation analysis

To identify potentially important teleost hosts for Arctic and Pacific lampreys, I investigated positive associations between lamprey CPUE and potential host CPUE, a relationship expected for hosts that are important to lampreys, using nonparametric Spearman's rank-order correlation (Hollander and Wolfe 1973). For this portion of the analysis, only regions with three or more stations sampled during each year were included. Additionally, regions in which lampreys were rarely captured, less than 5% of stations, were excluded to avoid including excessive zeros in the data.

The potential hosts investigated were selected using the results of the previously described SIMPER routine and prior knowledge of lamprey feeding in the eastern Bering Sea. Included teleost groups had a greater average CPUE for the High lamprey catch group compared to the Low lamprey catch group in the SIMPER analysis, contributed more than two percent to the dissimilarity between these groups, and consistently contributed to the dissimilarity, defined here as having a dissimilarity divided by standard deviation that is greater than one. Substantial evidence indicates that Pacific Cod are frequently found with Pacific Lamprey wounds (see Chapter 2); therefore, this species was included in the benthic survey analysis regardless of the SIMPER results.

Summarized lamprey and teleost catch data were analyzed differently by survey to account for differences in the number of years sampled. To examine general trends between teleosts and lampreys, I paired lamprey CPUE and potential host CPUE for all included year-region combinations and tested for a positive relationship. Because the epipelagic survey sampled ten years, compared to five years for the benthic survey, I was

able to further analyze correlations between lamprey CPUE and suspected host CPUE for each included region separately. Significance was determined at an alpha equal to 0.05 divided by the number of simultaneous tests occurring, reducing the chance of making a Type I error associated with multiple comparisons.

1.4 Results

Distributions of Arctic and Pacific lampreys in the eastern Bering Sea differed vertically within the water column and geographically. In the study area, Arctic Lampreys were captured at 19.0% of epipelagic stations and 0.0% of benthic stations, whereas Pacific Lampreys were captured at < 0.1% of epipelagic stations and 8.3% of benthic stations. Arctic Lampreys were predominantly captured in regions on the inner and middle continental shelf and in northern region of the study area (Figure 1.2), whereas Pacific Lampreys were predominantly captured in regions along the continental slope (Figure 1.3). Arctic and Pacific lampreys were never captured at the same station, but both species were captured in the north middle shelf region during the 2002 epipelagic survey. Among sampled years in the study region, 2002 exhibited the highest annual mean lamprey CPUE and proportion of stations with lampreys present for both Arctic and Pacific lampreys, and lamprey catches were relatively depressed in subsequent years (Tables 1.1 and 1.2).

1.4.1 Ordination analysis

Ordination of teleost CPUE data for year-region combinations allowed for the detection of differences in fish assemblages in regions with and without lampreys present. Teleost CPUE data from the epipelagic survey clustered by High and Low Arctic

Lamprey catch groups. These clusters were evident in a two-dimensional NMDS plot (Kruskal's stress value = 0.22), but due to the high stress value I further examined a three-dimensional NMDS plot (Kruskal's stress value = 0.14; Figure 1.4). Latitudinal and longitudinal gradients were evident in epipelagic fish assemblages occurring in the eastern Bering Sea, suggesting regional consistency in fish assemblages over time. Fish assemblages were significantly different between High and Low Arctic Lamprey catch groups (ANOSIM: $R = 0.158$; $P < 0.001$), though the Low group did exhibit more within-group variability of fish assemblages compared to the High group (MVDISP: 1.15 and 0.64, respectively). The NMDS plot further illustrated that the Low Arctic Lamprey group included a few year-region combinations that had relatively great Pacific Herring CPUE and were similar to the High group, but the majority of the Low group that was distinct from the High group had little or no Pacific Herring CPUE. A SIMPER routine identified that Pacific Herring was the most distinguishing teleost group between High and Low Arctic Lamprey catch groups. The High group had a relatively greater average abundance of Pacific Herring, juvenile Chum Salmon, juvenile Chinook Salmon *Oncorhynchus tshawytscha*, juvenile Coho Salmon *O. kisutch*, and juvenile Pink Salmon, and the Low group had a relatively higher abundance of Walleye Pollock *Gadus chalcogrammus*, immature/mature Chum Salmon, and immature/mature Chinook Salmon (Table 1.3).

Teleost CPUE data from the benthic survey clustered by High and Low Pacific Lamprey catch groups. Overall, benthic fish assemblages in the eastern Bering Sea exhibited both latitudinal and depth gradients, evident from a two-dimensional NMDS

plot (Kruskal's stress value = 0.08), and reflecting regional consistency of fish assemblages (Figure 1.5). Fish assemblages were significantly different between High and Low Pacific Lamprey catch groups (ANOSIM: $R = 0.48$; $P < 0.001$), although the Low group exhibited more within-group variability of fish assemblages than the High group (MVDISP: 1.01 and 0.90, respectively). A SIMPER routine identified the High Pacific Lamprey catch group to have a relatively higher abundance of Pacific Ocean Perch *Sebastes alutus*, Arrowtooth Flounder *Atheresthes stomias*, Flathead Sole *Hippoglossoides elassodon*, Greenland Halibut *Reinhardtius hippoglossoides*, Kamchatka Flounder *Atheresthes evermanni*, and Rex Sole *Glyptocephalus zachirus* compared to the Low group. Additionally, Giant Grenadier *Albatrossia pectoralis*, Popeye Grenadier *Coryphaenoides cinereus*, and Shortspine Thornyhead *Sebastolobus alascanus* were abundant in the High group and completely absent from the Low group. The Low Pacific Lamprey catch group had a relatively higher abundance of Walleye Pollock, Yellowfin Sole *Limanda aspera*, Northern Rock Sole *Lepidopsetta polyxystra*, Alaska Plaice *Pleuronectes quadrituberculatus*, and Pacific Cod *Gadus macrocephallus* compared to the High group (Table 1.4).

1.4.2 Lamprey and host correlation analysis

The regions in which three or more epipelagic stations were sampled for each year included in this study and, at which Arctic Lampreys were present at a minimum of 5% of the stations, were the following: south Bering Strait, north inner, midnorth inner, south inner, St. Matthews, and south middle (Figure 1.1). Of the five potential hosts suggested by the epipelagic SIMPER analysis results, Arctic Lamprey CPUE was

positively and significantly correlated with the CPUE of Pacific Herring and juvenile Chinook Salmon ($P < 0.01$), and although not significant at $\alpha = 0.01$ (adjusted for the occurrence of five simultaneous tests), Arctic Lamprey CPUE was positively correlated with the CPUE of juvenile Chum, Coho, and Pink Salmon ($P < 0.02$; Table 1.3). Region-specific analysis indicated that no suspected hosts had a significantly positive relationship with Arctic Lamprey CPUE for the south Bering Strait, north inner, St. Matthews, or south middle regions (Table 1.5). However, Arctic Lamprey CPUE was significantly and positively correlated with juvenile Chinook Salmon ($\rho = 0.93$, $P < 0.001$) and juvenile Pink Salmon ($\rho = 0.92$, $P < 0.001$) for the south inner region (Figure 1.6).

The regions in which three or more benthic stations were sampled for each year included in this study and, at which Pacific Lampreys were present at a minimum of 5% of the stations, were the off-shelf north and off-shelf southeast regions (Figure 1.1). The only identified potential hosts that were positively correlated with Pacific Lamprey CPUE were Pacific Cod, Greenland Halibut, Kamchatka Flounder, and Shortspine Thornyhead, although the CPUE of all potential hosts were not significantly correlated with Pacific Lamprey CPUE at $\alpha = 0.005$ (Table 1.4).

1.5 Discussion

Non-overlapping distributions of Arctic and Pacific lampreys in the eastern Bering Sea emphasize the unique life-history patterns of these two species. Arctic Lampreys were consistently found in epipelagic waters of northerly regions on the inner and middle continental shelf, and Pacific Lampreys were very rarely captured in epipelagic stations further west. Pacific Lampreys were consistently captured in benthic

waters along the continental slope, and Arctic Lampreys were never captured in the benthic trawl survey. In this study, Arctic and Pacific lampreys were never captured at the same station, further confirming the habitat separation of these species in the eastern Bering Sea. Additionally, the only time both species were captured in the same region (North Middle, epipelagic survey in 2002 that includes stations with one hour tows not included in this analysis), the location of the single station with Pacific Lamprey was located westward of the eleven stations with Arctic Lamprey present. These findings are consistent with previous compilations of single species distributions of anadromous lampreys in this region, placing Arctic lamprey distribution nearshore and Pacific Lamprey distribution near the continental slope (Orlov et al. 2008, 2014).

Juvenile salmonids and Pacific Herring were distributed in the same regions of the eastern Bering Sea as Arctic Lamprey. In general, Arctic Lampreys were not present in regions that lacked Pacific Herring, and the average Pacific Herring CPUE was more than double for year-region combinations in which Arctic Lamprey were present, suggesting an association between Arctic Lamprey distribution and Pacific Herring presence. In addition, four species of juvenile salmon (Chinook, Chum, Coho, and Pink salmon) had an average CPUE more than double in year-region combinations with Arctic Lamprey present, suggesting a similar association between Arctic Lamprey distributions and juvenile salmonid presence. This relationship is believed to be related to feeding because juvenile salmon and Pacific Herring have been observed with small lamprey wounds, thought to be inflicted by Arctic Lamprey, during BASIS surveys (J. Murphy, Alaska Fisheries Science Center, personal communication). Thus, Arctic Lamprey may be

distributing where Pacific Herring and juvenile salmon are more abundant. Alternatively, Arctic Lamprey, Pacific Herring, and juvenile salmon may all simply prefer shallow nearshore areas, resulting in the observed coincidental overlap of their distributions. Regardless, Pacific Herring and juvenile salmon are likely to be impacted by Arctic Lamprey in the eastern Bering Sea because overlapping distributions make them available hosts. This hypothesis is supported by the positive rank-order correlation between the CPUE of Arctic Lamprey and the CPUE of all five potential teleost hosts. I infer that Arctic Lamprey distribution in the eastern Bering Sea is largely a function of the presence of one or more of the five potential hosts identified, while the density of Arctic Lamprey is related to the abundance of those hosts.

In the south inner region, Arctic Lamprey CPUE was significantly and positively correlated with both juvenile Chinook Salmon ($P < 0.001$) and juvenile Pink Salmon CPUE ($P < 0.001$), suggesting that Arctic lampreys are only found in the south inner region when potential hosts are there and are more abundant when their hosts are more abundant (Figure 1.6). This overall trend was evident in the south inner region for the CPUE of Arctic Lamprey and the remaining three potential hosts identified (Pacific Herring and juvenile Chum and Coho salmon), although these relationships were not found to be significantly correlated. Little or no potential hosts were present in the south inner region during 2010, 2011, and 2012, likely reflecting the change in timing of the southern Bering Sea BASIS survey beginning in 2009 rather than declines in the abundance of potential hosts. However, there was a small catch of potential hosts and Arctic Lamprey in 2009, following the change in survey timing, and a lack of hosts and

Arctic Lamprey in 2006 prior to the change in survey timing, suggesting that Arctic Lamprey vary in concordance with Pacific Herring and juvenile salmonids. The overall lack of region-specific correlation found for northerly regions analyzed could be from the fact that Arctic Lamprey and the potential hosts identified are ubiquitous in these regions during the sampled periods.

The results of this study indicate that the continental slope is an important habitat for Pacific Lamprey, but there were no significant positive correlations between the CPUE of any of the ten potential hosts and Pacific Lamprey. The diversity of fish present on the continental slope (68 teleost groups were present at > 5% of stations) may reflect a great diversity of hosts available to Pacific Lamprey, such that no specific species drive lamprey density. Teleosts that utilize the continental slope, but are not likely to drive Pacific Lamprey density, as suggested by negative or near-zero correlation coefficients, include Arrowtooth Flounder, Flathead Sole, Rex Sole, Giant Grenadier, Popeye Grenadier, Pacific Ocean Perch, Kamchatka Flounder, and Shortspine Thornyhead (Table 1.4). Pacific Cod and Greenland Halibut did have the greatest positive correlation coefficients (Table 1.4), though not significant, making these species the most likely hosts associated with Pacific Lamprey in the eastern Bering Sea. In the western Bering Sea, Pacific Cod and Greenland Halibut are suspected of being important hosts for Pacific Lamprey (Orlov et al. 2009), further supporting the hypothesis that they are important to Pacific Lamprey in the eastern Bering Sea. Interestingly, Pacific Cod typically had a higher CPUE in continental shelf regions that lacked Pacific Lampreys in this study, despite evidence that Pacific Lamprey parasitize this species along the

continental slope in the eastern Bering Sea (see Chapter 2). However, this species is known to spawn on the outer continental shelf in waters between 100 and 200 m from March to April (Neidetcher et al. 2014), and lamprey parasitism may be occurring during these episodic spawning events not captured during the time frame of this study.

Feeding behavior can differ among parasitic lamprey species, and this could play a role in host selection and lamprey distribution. Lampreys that feed on blood are expected to select larger hosts that can sustain longer feeding events, whereas lampreys that feed on flesh target smaller hosts that are easily killed and more abundant (Beamish 1980; Renaud et al. 2009). Pacific Lampreys are known to consume both flesh and blood of their hosts (Renaud et al. 2009), and the association of this species with large groundfish (Greenland Halibut and Pacific Cod) along the continental slope of the eastern Bering Sea is consistent with a lamprey that feeds on blood. In contrast, Arctic Lampreys are inferred to be flesh feeders (Renaud et al. 2009), and the observed association between Arctic Lamprey distribution and small pelagic fish (Pacific Herring and juvenile salmonids) is consistent with the expected feeding behavior of a flesh-feeding lamprey. Differing feeding behaviors could be a possible basis for differences in lamprey-host interactions, and thus separated marine distributions observed in this study, but it is also possible that restricted migratory ranges of lampreys in the eastern Bering Sea has limited the types of hosts available for feeding, giving rise to these species-specific feeding behaviors in the region.

Another possible mechanism contributing to the longitudinal separation of Arctic and Pacific lamprey distributions is the eastern Bering Sea cold pool, which annually

forms on the middle continental shelf. The cold pool does restrict the dispersion of a variety of fish that lampreys may parasitize such as Pacific Herring, Walleye Pollock, Pacific Cod, and Capelin *Mallotus villosus* (Hollowed et al. 2012; Stabeno et al. 2012). In this study, Arctic and Pacific lampreys both had relatively broad distributions during the warm year of 2002, which was associated with a small cold pool extent. In contrast, during the cold year of 2010, lamprey distributions were relatively restricted, which was associated with a vast cold pool extent (Stabeno et al. 2012). One possible reason for the observed separation of the distributions of Arctic and Pacific lampreys is that the cold pool is not directly limiting lamprey movements, but rather, the hosts on which lampreys are feeding are restricted by this cold water mass, and lampreys remain where there are abundant hosts. Alternatively, Arctic Lamprey movements may be limited to nearshore environments while Pacific Lamprey movements allow for offshore excursions, and the cold pool could be one mechanism limiting which hosts are available in these different habitats.

A glimpse of a finer-scale understanding of the distributions of Arctic and Pacific lampreys and associations with potential host fishes can be provided through examination of the north middle shelf region from the 2002 epipelagic survey, in which Arctic and Pacific lampreys were both captured (note that the duration of some of the tows was one hour and not included in the main analysis). Of the 13 stations sampled, Arctic Lampreys were captured at 11 sites and Pacific Lampreys were captured at one site. The single station with Pacific Lamprey also produced the maximum Walleye Pollock CPUE in the region. However, a quantitative understanding of the relationship between Pacific

Lamprey and Walleye Pollock in pelagic habitats is not possible from this analysis because Pacific Lamprey were excluded from the epipelagic analysis. Of the 11 stations at which Arctic Lamprey were captured, the one site with the maximum Arctic Lamprey CPUE co-occurred with the maximum Capelin CPUE. This suggests that Capelin abundance may be associated with Arctic Lamprey distribution at finer scales, whereas the broader scale regional analysis did not indicate this possibility. One possible reason for this discrepancy is the high annual variability in Capelin abundance observed in epipelagic surveys, making this species an available host when abundant, but not when rare. Because Arctic and Pacific lampreys likely feed on a variety of hosts, localized or annual abundance of some fishes may actually be related to lamprey distributions at finer scales yet go unnoticed at broader scales, precluding those potential lamprey-host interactions from being inferred by the approach utilized in this study.

One potential limitation to the interpretation of the results is that epipelagic and benthic surveys utilized in this study employed different sampling gear. The smaller mesh used in the epipelagic survey (1.2 cm) is certainly more effective at capturing both Arctic and Pacific lampreys compared to the larger mesh used in the benthic survey (3.2 cm). The absence of Pacific Lamprey in inner and middle continental shelf epipelagic trawls indicates that this species is not actively using this environment. However, Pacific Lampreys were captured in five epipelagic trawls conducted over the outer continental shelf and continental slope despite the low sampling effort, suggesting that Pacific Lampreys are occasionally utilizing epipelagic waters in these regions, as well as the benthic environment. The benthic trawl survey does occasionally capture small fishes

such as Pacific Herring, Capelin, and myctophids (Myctophidae), and if Arctic Lamprey were frequently utilizing the benthos, I would expect at least sporadic catches of this species. Because no Arctic Lampreys were captured in benthic trawl surveys, even in regions where Arctic Lamprey were known to be in pelagic waters, I believe that this species rarely inhabits benthic habitats. As such, I do not believe that the differences between trawls used in these surveys contributed to the results described herein, rather the presence and absence of lampreys accurately reflects habitat utilization by species.

An additional limitation of this study is that surveys were limited spatially and temporally, potentially missing important seasonal or episodic shifts in distributions. Survey data used in this analysis did not include nearshore estuarine habitats and would not capture lampreys utilizing these habitats, but lampreys are often found feeding in estuaries in other regions. For example, Arctic Lampreys in the western Bering Sea were estimated to consume 75% of Pink and Chum salmon smolts in the Amur river estuary (Novomodnyy and Belyaev 2002), and the Western River Lamprey fed on Pacific Herring and Pacific salmon smolts in the nearshore Fraser River plume (Beamish and Neville 1995). It is expected that similar predation events on juvenile salmon occur in the western Alaska river deltas due to the close proximity of Arctic Lampreys to the estuaries of the Yukon and Kuskokwim Rivers, and sampling of these habitats could find concentrations of lampreys not identified by this study. Additionally, no sampling occurred in any year from November through May, and distributions and associations of lampreys and potential hosts reported herein may not hold true during these colder months.

In the future, several improvements can be incorporated into research of adult trophic-phase lampreys. Analysis into the relative importance of different hosts should be pursued in more detail, with lamprey digestive tract analysis as one possible method for investigating contributions of different species to lamprey diets. This study found correlation between lampreys and potential hosts, but a diet analysis would be able to test the proposed hypothesis that feeding is the cause for this correlation, bolstering the argument that association is related to feeding. Furthermore, lamprey sampling components should be included in estuarine and nearshore research occurring in Alaska, as this is believed to be an important habitat for these species. To determine the rivers of origin of adult lampreys captured in the Bering Sea which may aid in explaining the nearshore distributions of Arctic Lamprey and the magnitude of Pacific Lamprey movements, genetic and tagging studies should be pursued. Finally, the NMFS Observer program provides a platform which already captures and records lampreys in the eastern Bering Sea (AFSC 2013), and efforts should be made to confirm species identification using dentition, an easily distinguishable characteristic for separating Arctic and Pacific lampreys (see Chapter 2).

With the continuation of lamprey exploitation and evident declines in many lamprey populations, it is important to understand all life history stages of parasitic, anadromous lampreys, and not just those occurring in freshwater. The role of the adult trophic phase in shaping lamprey populations has not been well studied, but host availability has been suggested as potentially limiting the number of spawning adults returning to rivers (Luzier et al. 2011, Murauskas et al. 2013). Further inference of

lamprey-host interactions through the study of distributions can aid in understanding which regions and host species are likely important to anadromous lampreys while in the ocean. If the adult trophic phase is important to lamprey survival and health, conservation and restoration programs will need to consider factors occurring during the adult trophic phase in their plans. For example, restoration efforts are underway for the Pacific Lamprey in the U.S. Pacific Northwest (Luzier et al. 2011), but we do not currently know where or on which hosts these animals are feeding while in the ocean. This study is an initial step towards understanding the adult trophic phase of Arctic and Pacific lampreys in the eastern Bering Sea, showing that Pacific Lamprey and Arctic Lamprey inhabit different regions, occur with different fish assemblages, and are thus likely to parasitize different fishes. As such, these two species will be impacted differently by stressors such as commercial fisheries, climatic shifts, or a warming ocean. Going forward, resource managers will need to consider and reconcile these differences to establish effective measures which support the conservation of Arctic and Pacific lampreys when needed, sustaining harvests of these species for generations to come.

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1.8 Figures

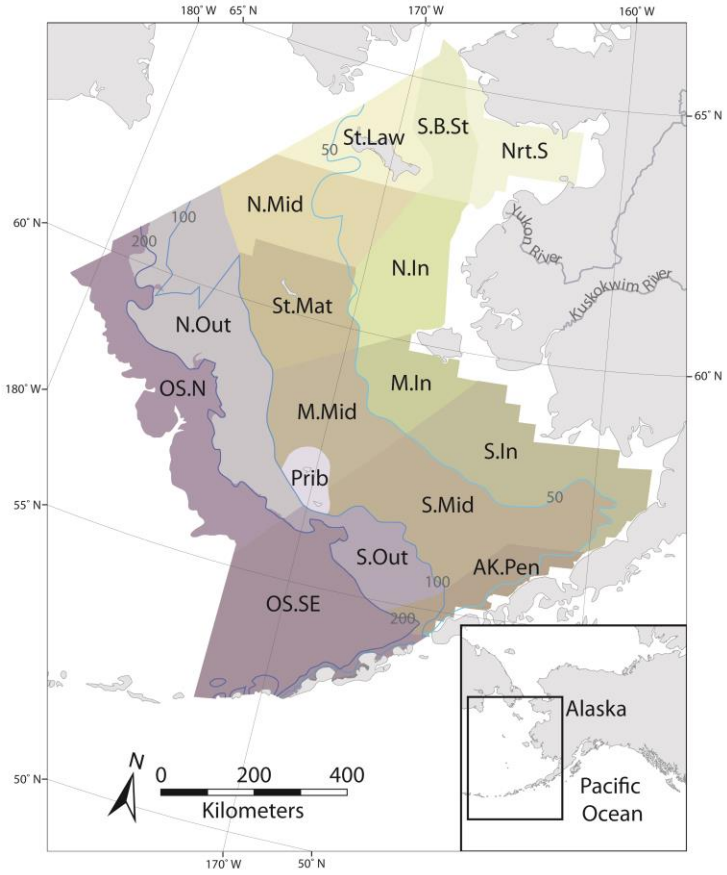

Figure 1.1. Map of Bering Sea Integrated Ecosystem Research Program regions used for summarizing lamprey and teleost CPUE data with map extent shown as a rectangle in lower right inset (Source: Ortiz et al. 2012). Isobaths are shown for 50-, 100-, and 200-m depths. Abbreviated region names for the inner continental shelf are S.B.St = south Bering Strait, Nrt.S = Norton Sound, N.In = north, M.In = midnorth, and S.In = south; middle continental shelf are St.Law = St. Lawrence, N.Mid = north, St.Mat = St. Matthews, M.Mid = midnorth, S.Mid = south, and AK.Pen = Alaska Peninsula; outer continental shelf are N.Out = north, Prib = Pribilofs, and S.Out = south; and off-shelf are OS.N = north and OS.SE = southeast.

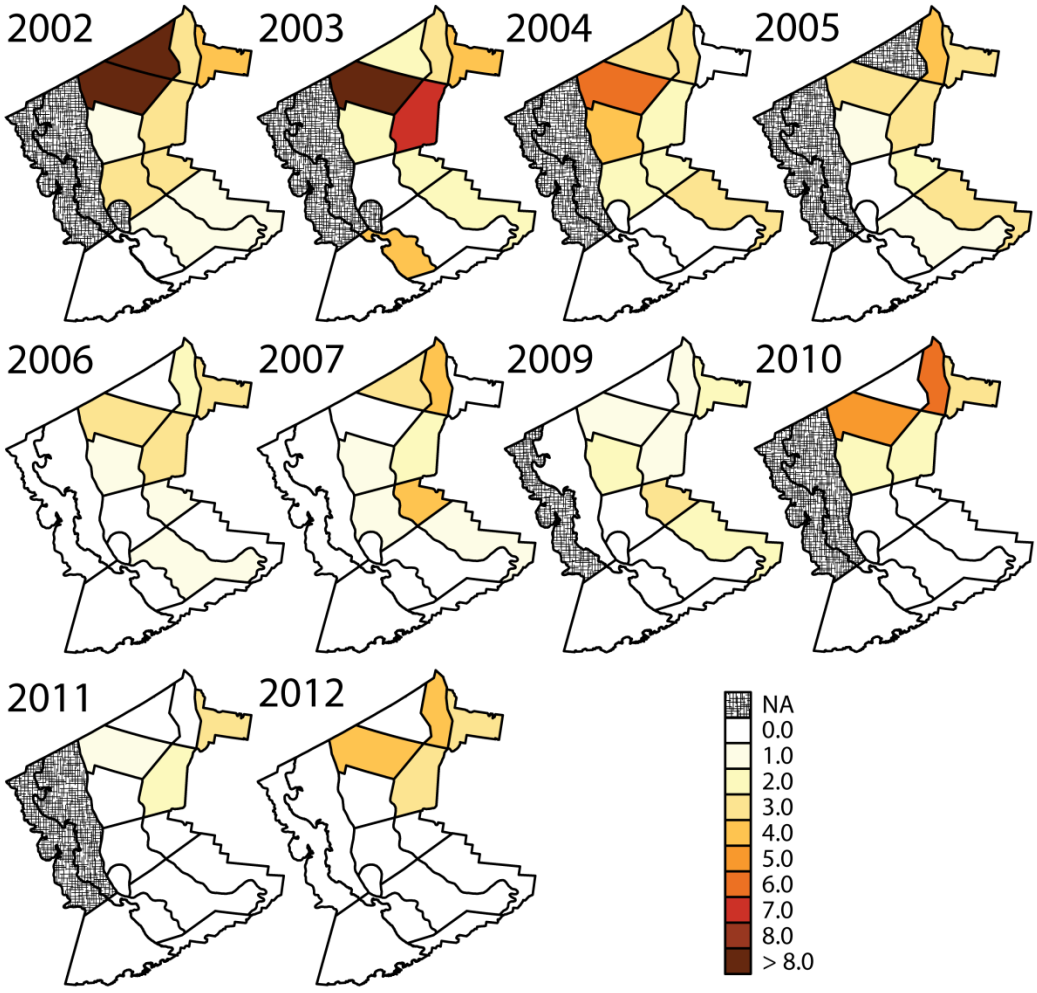

Figure 1.2. Annual maps of Arctic Lamprey epipelagic distribution (except 2008) depicting the average CPUE (kg/ha $\times 10^{-4}$). The extent of annual maps is the BSIERP regions described in Figure 1.1. Note that prior to 2009, this survey was conducted by one vessel, and beginning in 2009, two vessels sampled concurrently changing the timing of sampling in some regions.

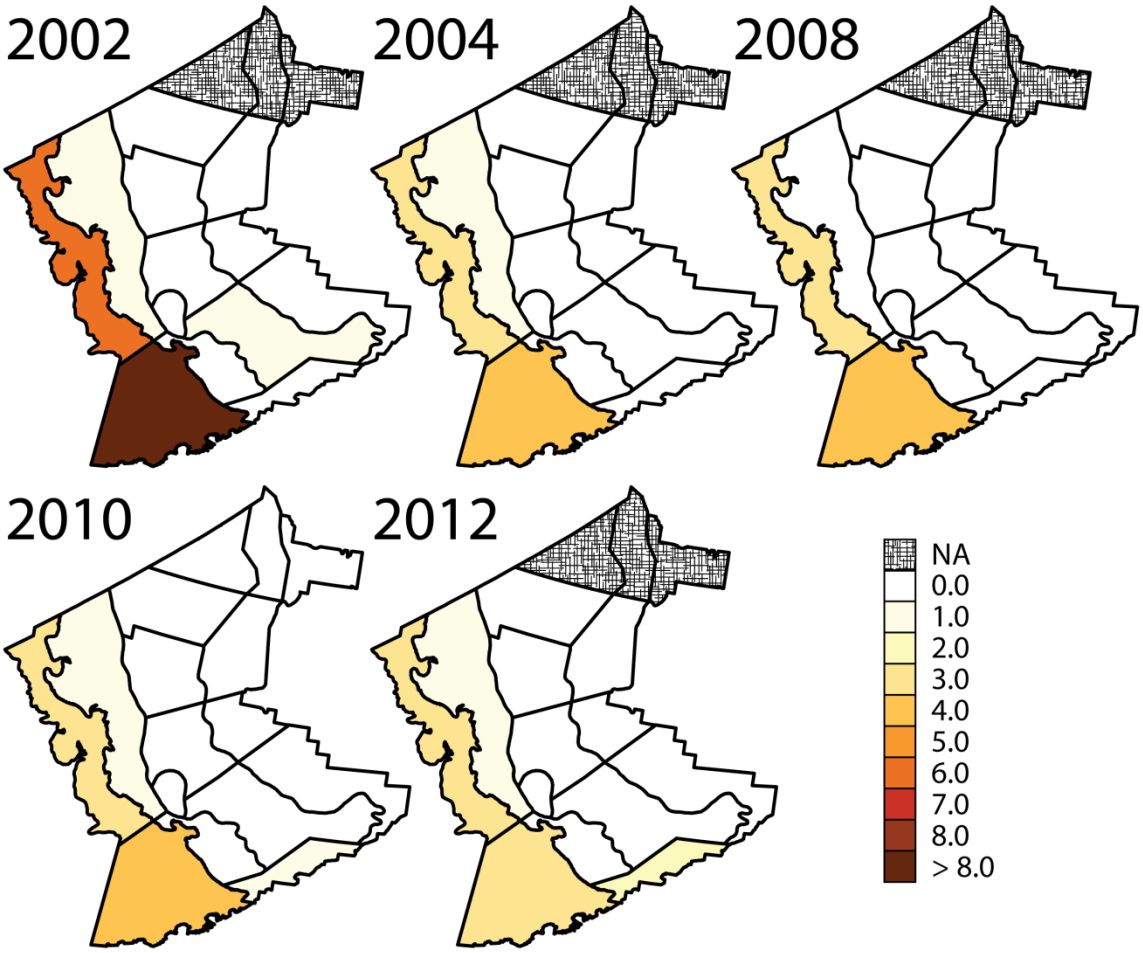

Figure 1.3. Biennial maps of Pacific Lamprey benthic distribution (except 2006) depicting the average CPUE (kg/ha $\times 10^{-2}$). The extent of biennial maps is the BSIERP regions described in Figure 1.1.

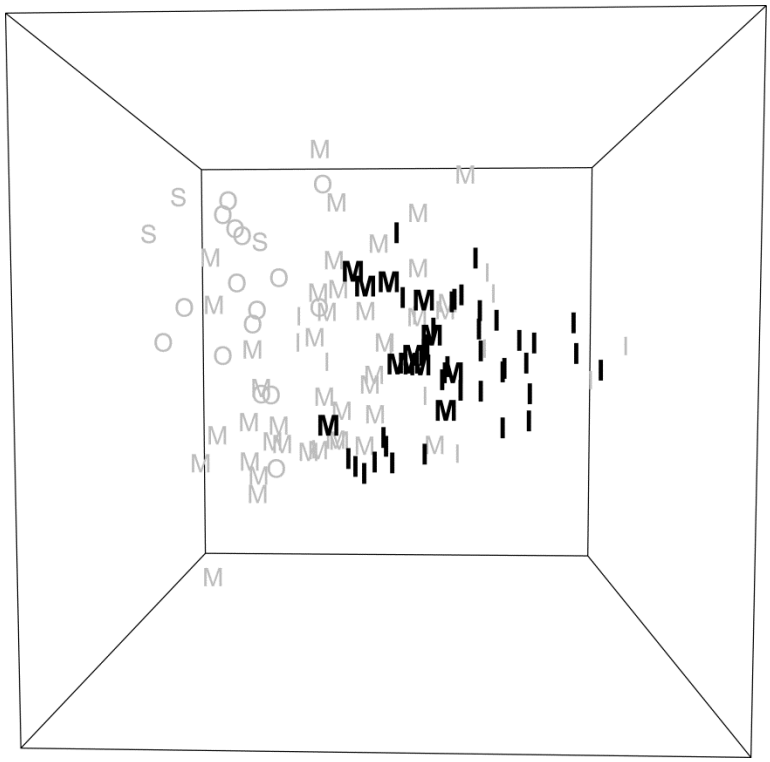

Figure 1.4. Nonmetric multidimensional scaling (NMDS) ordination of epipelagic fish reduced to three dimensions (Kruskal's stress = 0.14) and based on a Bray-Curtis similarity matrix of square-root-transformed teleost CPUE data. Year-region combinations with two or more Arctic Lampreys present are shown in black and those with fewer than two Arctic Lampreys present are shown in gray. Letters refer to the location of each region on the continental shelf as described in Figure 1.1: inner (I), middle (M), outer (O), and off-shelf (S).

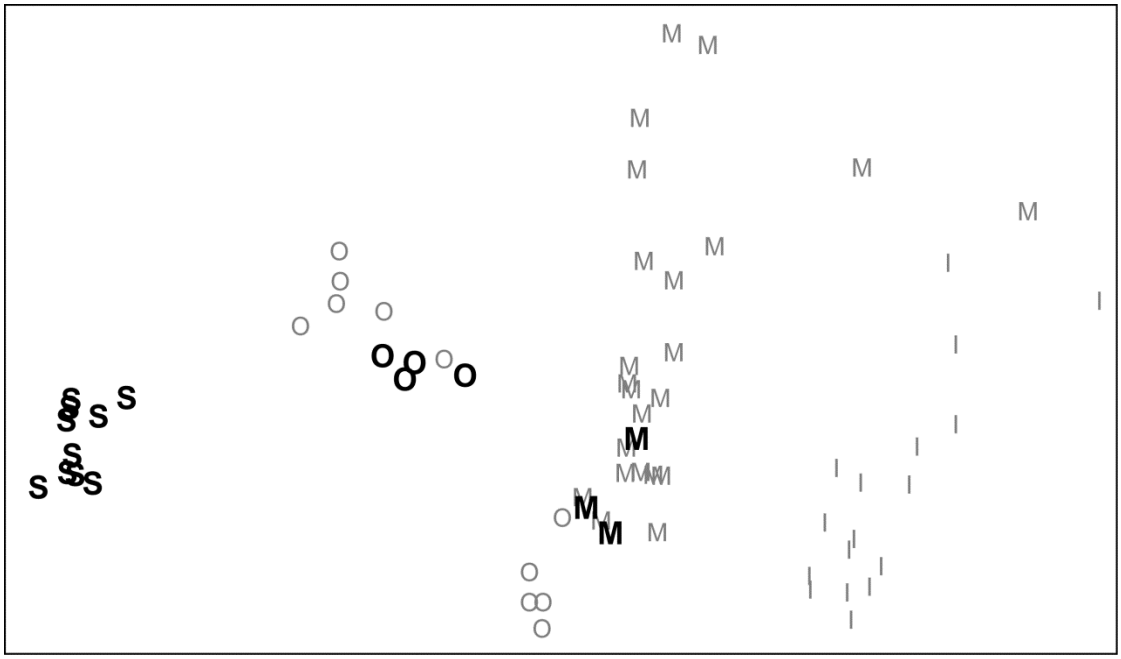

Figure 1.5. Nonmetric multidimensional scaling (NMDS) ordination of benthic fish reduced to two dimensions (Kruskal's stress = 0.08) and based on a Bray-Curtis similarity matrix of square-root-transformed teleost CPUE data. Year-region combinations with at least one Pacific Lamprey present are shown in black and those with no Pacific Lamprey present are shown in gray. Letters refer to regions location on the continental shelf described in Figure 1.1: inner (I), middle (M), outer (O), and off-shelf (S).

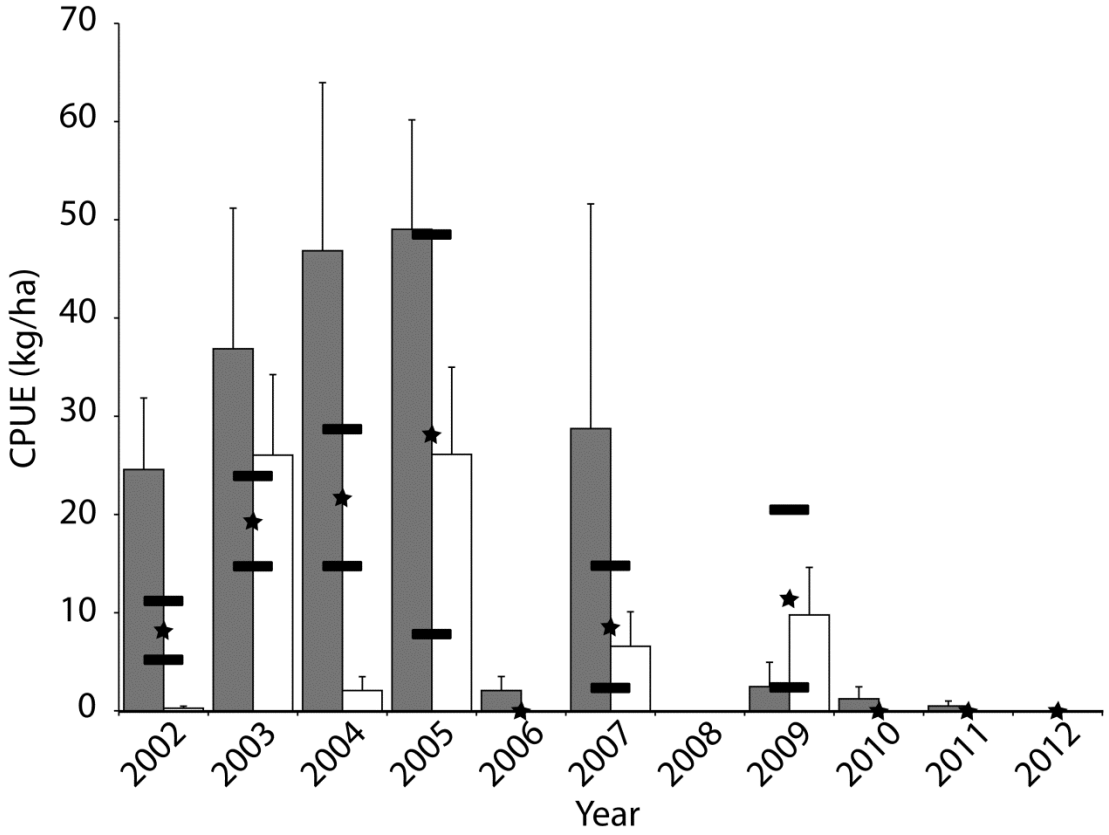

Figure 1.6. Mean CPUE of Arctic Lamprey and hosts in epipelagic south inner region of the eastern Bering Sea where black stars and horizontal bars indicate Arctic Lamprey ± SE ($\times 10^{-4}$), gray vertical bars indicate juvenile Chinook Salmon + SE ($\times 10^{-3}$), and white vertical bars indicate juvenile Pink Salmon + SE ($\times 10^{-3}$).

1.9 Tables

Table 1.1. Frequency of epipelagic trawl stations sampled by year and region (region locations and abbreviations described in Figure 1.1). Values in light gray indicate a year-region combination that was removed prior to teleost CPUE analysis because of insufficient sampling. The final two rows and columns list the percent of stations with Arctic Lamprey present (%AL) and the average Arctic Lamprey CPUE in kg/ha ($\times 10^{-5}$).

Region	02	03	04	05	06	07	09	10	11	12	%AL	CPUE
S.B.St[c]	15	13	7	4	7	12	8	12	11	12	38.6	25.5
Nrt.S	5	3	5	2[a]	6	4	7	12	11	8	38.1	22.2
N.In[c]	15	15	16	16	17	13	15	15	17	14	35.3	23.1
M.In[c]	14	7	10	10	9	10	3	8	4	9	28.6	14.6
S.In[c]	30	29	19	18	14	16	7	15	10	11	24.9	11.5
St.Law	12	4	9	-	4	8	2	2	3	2	32.6	30.9
N.Mid	7	1[a]	15	9	9	8	8	10	7	1[a]	45.3	41.9
St.Mat[c]	5	9	10	15	9	10	7	8	5	4	18.3	12.2
M.Mid	2[a]	10	10	6	15	15	8	12	12	16	3.8	1.8
S.Mid	30	27	25	24	30	27	14	22	21	25	1.2	0.7
AK.Pen	12	11	5	7	5	5	3	8	5	7	0.0	0.0
N.Out	-	-	-	-	5	2	6	-	-	3	0.0	0.0
Prib	-	-	2	2	4	4	1	1	4	4	0.0	0.0
S.Out	1	4	8	10	12[b]	10	4	17	10	10	1.2	1.5
OS.N	-	-	-	-	3	1	-	-	-	1	0.0	0.0
OS.SE	1	1	1	1	7	6	2	2	1	2	0.0	0.0
%AL	33.6	27.6	30.3	14.5	12.8	14.6	13.7	14.6	13.2	11.6		
CPUE	25.5	18.3	18.9	11.6	6.9	9.0	6.6	11.3	4.8	8.4		

[a]Indicates at least one station contained Arctic Lamprey, but was not included in further analysis.

[b]Indicates at least one station contained Pacific Lamprey, but was not further examined for this species.

[c]Indicates regions included in Spearman's rank-order correlation analysis between the CPUE of Arctic Lamprey and that of potential hosts.

Table 1.2. Frequency of benthic trawl stations sampled by year and region (region locations and abbreviations described in Figure 1.1). Dashes in light gray indicate a year-region combination that was removed prior to teleost CPUE analysis because of no sampling effort. The final two rows and columns list the percent of stations with Pacific Lamprey present (%PL) and the average Pacific Lamprey CPUE in kg/ha ($\times 10^{-3}$).

Region	02	04	08	10	12	%PL	CPUE
S.B.St	-	-	-	23	-	0.0	0.0
Nrt.S	-	-	-	22	-	0.0	0.0
N.In	7	7	7	40	7	0.0	0.0
M.In	24	24	24	24	24	0.0	0.0
S.In	55	55	54	55	55	0.0	0.0
St.Law	-	-	-	25	-	0.0	0.0
N.Mid	13	13	13	46	13	0.0	0.0
St.Mat	43	43	43	45	42	0.0	0.0
M.Mid	41	41	41	41	41	0.0	0.0
S.Mid	64	64	62	64	63	0.3	0.4
AK.Pen	19	19	8	19	20	3.5	4.9
N.Out	76	75	75	75	79	1.3	1.2
Prib	14	15	14	14	14	0.0	0.0
S.Out	22	23	11	24	25	0.0	0.0
OS.N[a]	72	101	101	97	95	23.4	27.6
OS.SE[a]	66	126	97	100	82	27.0	41.1
%PL	11.4	7.8	8.7	7.3	6.8		
CPUE	18.4	12.6	8.6	8.6	9.3		

[a]Indicates regions included in Spearman's rank-order correlation analysis between the CPUE of Pacific Lamprey and that of potential hosts.

Table 1.3. Epipelagic similarity percentage (SIMPER) and correlation results, enumerating relative dissimilarity in epipelagic fish assemblages between year-region combinations with and without Arctic Lamprey present. Average transformed CPUE in the Low Arctic Lamprey catch group (Low), average transformed CPUE in the High Arctic Lamprey catch group (High), and average dissimilarity between these groups (Av. Diss) are listed for each species with a dissimilarity divided by standard deviation (Diss/SD) greater than 1.0 and contribution to the overall dissimilarity (%) greater than 2%. Bolded species were suspected hosts of Arctic Lamprey, and values of Spearman's correlation coefficient rho (ρ) are listed for comparisons between Arctic Lamprey CPUE and the CPUE of the listed species. Asterisks denote significant positive correlation between CPUE of Arctic Lamprey and the CPUE of suspected host fishes ($P < 0.01$).

Species	Low	High	Av. Diss	Diss/SD	%	ρ
Pacific Herring	0.36	0.83	12.61	1.29	19.24	0.49*
Chum Salmon	0.54	0.25	7.68	1.02	11.72	
Walleye Pollock	0.40	0.29	7.48	1.01	11.41	
Juvenile Chum Salmon	0.10	0.24	4.03	1.24	6.16	0.32
Juvenile Pink Salmon	0.08	0.16	2.63	1.17	4.01	0.32
Chinook Salmon	0.14	0.12	2.62	1.07	4.00	
Juvenile Coho Salmon	0.05	0.11	2.10	1.03	3.21	0.31*
Juvenile Chinook Salmon	0.03	0.12	2.08	1.44	3.17	0.48

Table 1.4. Benthic similarity percentage (SIMPER) and correlation results, enumerating the relative dissimilarity in benthic fish assemblages between year-region combinations with and without Pacific Lamprey present. Average transformed CPUE in the Low Pacific Lamprey catch group (Low), average transformed CPUE in the High Pacific Lamprey catch group (High), and average dissimilarity (Av. Diss) are listed for each species with a dissimilarity divided by standard deviation (Diss/SD) greater than 1.0 and contribution to the overall dissimilarity (%) greater than 2%. Bolded species were suspected hosts of Pacific Lamprey, and values of Spearman's correlation coefficient rho (ρ) are listed for comparisons between Pacific Lamprey CPUE and the CPUE of the listed species; no significant relationships were detected ($P < 0.005$ level).

Species	Low	High	Av. Diss	Diss/SD	%	ρ
Giant Grenadier	0.00	7.37	7.73	1.10	11.66	-0.53
Walleye Pollock	6.62	6.21	5.49	1.30	8.28	
Yellowfin Sole	5.12	1.49	5.43	1.35	8.20	
Northern Rock Sole	5.56	1.61	5.13	1.27	7.75	
Pacific Ocean Perch	0.33	4.30	4.53	1.36	6.84	-0.64
Arrowtooth Flounder	1.64	4.34	3.56	1.74	5.37	-0.14
Alaska Plaice	2.97	0.65	2.86	1.58	4.32	
Popeye Grenadier	0.00	2.31	2.44	1.16	3.68	-0.36
Flathead Sole	2.23	3.09	2.27	1.48	3.43	-0.30
Greenland Halibut	0.20	1.94	1.97	1.68	2.98	0.54
Pacific Cod	3.26	2.25	1.88	1.39	2.84	0.36
Kamchatka Flounder	0.46	2.09	1.88	1.60	2.83	0.18
Shortspine Thornyhead	0.00	1.67	1.79	1.12	2.71	0.21
Rex Sole	0.30	1.51	1.43	2.04	2.16	-0.08

Table 1.5. Spearman's correlation coefficients (ρ) of suspected host fishes by region (region locations and abbreviations described in Figure 1.1), where comparisons are between the CPUE of Arctic Lamprey and the CPUE of suspected host fishes. Asterisks denote significant positive correlation between CPUE of Arctic Lamprey and the CPUE of suspected host fishes ($P \leq 0.002$).

Region	Pacific Herring	Juvenile Chinook Salmon	Juvenile Chum Salmon	Juvenile Coho Salmon	Juvenile Pink Salmon
M.In	0.56	0.62	0.46	0.74	0.56
N.In	0.54	-0.42	0.44	0.12	-0.15
S.B.S	-0.20	0.12	-0.41	-0.30	-0.33
S.In	0.64	0.93*	0.56	0.72	0.92*
St.Mat	0.56	0.62	0.46	0.74	0.56

CHAPTER 2:

Interactions between lampreys and Pacific Cod in the eastern Bering Sea[1]

2.1 Abstract

Interactions between adult anadromous lampreys and their hosts are not well understood, even though lampreys pose a potential threat to species targeted by large-scale commercial fisheries. Arctic Lamprey *Lethenteron camtschaticum* and Pacific Lamprey *Entosphenus tridentatus* are anadromous species found in the eastern Bering Sea, and lamprey parasitism is evident on Pacific Cod *Gadus macrocephalus* near the continental slope. To examine this parasitic interaction, I explored similarities between the morphology of lamprey oral discs and lamprey wounds on Pacific Cod, examined relationships between lamprey wounding rates and Pacific Cod length, and explored healing patterns in the severity and location of lamprey wounds. In total, 8,746 Pacific Cod were scanned for lamprey wounds, of which 4.9% had at least one. The circular shape of lamprey wounds on Pacific Cod was similar to that of Pacific Lamprey oral discs, both differing from the oblong shape of Arctic Lamprey oral discs, which suggests that Pacific Lamprey were inflicting the wounds observed on Pacific Cod. Additionally, recent lamprey wounding was consistently more prevalent as Pacific Cod length increased, from 2% on fish < 65 cm to 3.5% on fish > 78 cm, possibly the result of size-dependent mortality experienced by Pacific Cod. Recently inflicted lamprey wounds that penetrated Pacific Cod muscle tissue were observed four times as often as superficial wounds that did not penetrate muscle tissue, but superficial wounds were twice as likely to be observed reaching a completely healed state, suggesting that Pacific Cod possibly

[1] Siwicke, K. A. 2014. Interactions between lampreys and Pacific Cod in the eastern Bering Sea. Prepared for submission to Transactions of the American Fisheries Society.

experience lamprey-related mortality when muscle tissue is penetrated during parasitism. However, the ratio of penetrating lamprey wounds observed in five different Pacific Cod body regions was consistent across four sequential healing stages, suggesting no difference in the likelihood of a lamprey wound to reach a completely healed state between vital and non-vital body regions. I believe that Pacific Lamprey parasitizing Pacific Cod may result in increased host mortality, which is likely resulting from indirect effects of parasitism such as increased vulnerability to predators and disease. This effect may be exacerbated for smaller hosts, which would explain why fewer small hosts are observed with wounds in samples compared to larger conspecifics. Parasitic interactions between native lampreys and their host fishes should not be overlooked as there is potential for this interaction to negatively affect host fish.

2.2 Introduction

Eighteen species of lamprey (Petromyzontiformes) undergo an adult trophic phase and are commonly referred to as parasitic, a term encompassing lampreys that feed on the blood, flesh, or blood and flesh of aquatic vertebrates (Potter and Hilliard 1987; Renaud et al. 2009; Renaud 2011). This parasitism is accomplished by a toothed oral disc used for securely attaching to hosts and a piston-like tongue used to bore into host tissue when feeding (Hardisty and Potter 1971). After a parasitic lamprey has detached from a host, an imprint of the oral disc remains as evidence of the interaction (Lennon 1954; King 1980), which can provide inference about the resulting consequences.

Frequently, parasitic interactions between lampreys and their hosts negatively impact individual hosts and entire fish stocks (Bence et al. 2003). The most severe consequence of lamprey parasitism is the mortality of the host. For example, Lake Sturgeon *Acipenser fulvescens* parasitized by Sea Lamprey *Petromyzon marinus* in a laboratory experienced 15% mortality attributed directly to the lamprey feeding (Patrick et al. 2009). In situ sampling of the Fraser River plume in British Columbia indicated Western River Lamprey *Lampetra ayresii* killed and consumed Pacific Herring *Clupea pallasii* and Pacific salmon *Oncorhynchus* spp. smolts (Beamish and Neville 1995). Similarly, Arctic Lamprey *Lethenteron camtschaticum* killed and consumed Chum Salmon *Oncorhynchus keta* and Pink Salmon *O. gorbuscha* smolts in the Amur River estuary, Russia (Novomodnyy and Belyaev 2002).

In addition to direct mortality, lamprey parasitism can cause deleterious sub-lethal impacts to hosts or result in the indirect mortality of hosts. For example, a lamprey

feeding event can cause anemia, leading to reduced growth and poor health of a host fish (Edsall and Swink 2001). While a lamprey is feeding, foraging ability and locomotion may be compromised, impacting the energy use of a host fish (Lennon 1954; Patrick et al. 2009). Additional impacts suffered by hosts include elevated stress levels and depressed blood chemistry parameters (e.g., hematocrit, hemoglobin, and plasma proteins; Sepulveda et al. 2012). In the northwestern Pacific Ocean, Sockeye Salmon *Oncorhynchus nerka*, Chinook Salmon *O. tshawytscha*, Pink Salmon, and Pacific Cod *Gadus macrocephalus* that were believed to be parasitized by a Pacific Lamprey *Entosphenus tridentatus* had lower gonado-somatic index values compared to healthy conspecifics (Pelenev et al. 2008; Pelenev et al. 2010). Indirect mortality can also follow the detachment of a feeding lamprey, as was the case for Lake Sturgeon that became more prone to secondary infections from fungus *Saprolegnia* spp. following lamprey parasitism (Patrick et al. 2009). Therefore, fishes that survive a parasitic lamprey feeding event may have compromised health, which can lead to a reduction in life span.

Beyond individual-level effects on host fishes, lampreys can have population-level effects. In the Laurentian Great Lakes, the invasive Sea Lamprey drastically reduced populations of native fish species such as Burbot *Lota lota* and Lake Trout *Salvelinus namaycush* (Stapanian et al. 2006) and had additional negative impacts on the rehabilitation of imperiled Lake Sturgeon stocks (Sutton et al. 2004). In the Fraser River plume, British Columbia, the estimated mortality induced by Western River Lamprey over two years was 359 million Pacific Herring and 90 million salmon smolts (Beamish and Neville 1995). Similarly, Arctic Lamprey feeding was the single greatest cause of

early stage mortality for Chum Salmon and Pink Salmon smolts in the Amur River estuary, Russia (Novomodnyy and Belyaev 2002). Therefore, lampreys pose a potentially great source of mortality to populations of the aquatic vertebrates they parasitize.

Lamprey parasitism does not impact all hosts equally, and a common factor that influences host selection and survival in lamprey-host dynamics is host size. In laboratory studies, the frequency of Sea Lamprey feeding events on individual hosts increased with host size (Farmer and Beamish 1973), and the number of lamprey feeding attempts significantly increased with host surface area (Cochran 1985). A theoretical comparison of Rainbow Trout *Oncorhynchus mykiss* and Lake Trout weight to lamprey weight showed that a 40:1 ratio is needed to survive, suggesting that host and lamprey size will influence survivorship (Farmer et al. 1975). In the western Bering Sea, Pacific Cod less than 50 cm did not exhibit any lamprey wounds, while lamprey wounds were common on larger conspecifics (Pelenev et al. 2010). This could imply that Pacific Cod less than 50 cm in length are not selected as lamprey hosts as often as larger individuals (Pelenev et al. 2010), or that this 50-cm length may be a threshold below which a Pacific Cod is not likely to survive a lamprey feeding event.

In addition to host size, the location of a lamprey feeding event on the body of a host fish appears to be an important factor for host survival. Lampreys typically select feeding locations to minimize being dislodged by the host fish, such as behind the pectoral fins where water velocity is reduced or anterior locations where there is less lateral movement (Farmer 1980; Cochran 1986; Bergstedt et al. 2001; Patrick et al. 2009). Additional factors thought to influence feeding location selection include

closeness of blood vessels to skin surface, presence of larger blood vessels, and areas where scales are reduced, thin, or absent (Farmer 1980; Cochran and Lyons 2010; Nichols and Tscherter 2011). On Pacific salmon, Pacific Lamprey wounds were observed more often in anterior and ventral body regions, proximal to vital organs, whereas Arctic Lamprey wounds were observed more often above the lateral line (Shevlyakov and Parensky 2010). In Pacific Cod examined for lamprey wounds in the western Bering Sea, over half of the fish were observed with wounds on the dorsal side (Pelenev et al. 2010). When feeding location coincides with vital regions of high blood supply, like the head and abdomen, the result can be higher mortality for the hosts, which may explain the lower prevalence of ventral wounds versus dorsal wounds often observed in situ (Beamish 1980; Cochran 1986; Pelenev et al. 2010).

Outside of the Laurentian Great Lakes, there is a paucity of information on lamprey-host interactions (Mesa and Copeland 2009). Native lampreys are believed to be in equilibrium with their hosts (Renaud 1997), but some native species do reduce host populations (Beamish and Neville 1995; Novomodnyy and Belyaev 2002), making the effects of native lamprey parasitism on fish stocks a potentially overlooked source of mortality. Arctic and Pacific lampreys are anadromous parasites that spend an adult trophic phase in the North Pacific Ocean and co-occur in the eastern Bering Sea with large-scale commercial fisheries including those targeting Walleye Pollock *Gadus chalcogrammus*, Pacific Cod, and Pacific Halibut *Hippoglossus stenolepis*. Both Arctic and Pacific lampreys are native species that evolved with the marine fishes they parasitize, but it is unknown which lamprey species interact with which commercially

valuable fishes and whether these interactions pose any impact to these fishes in the eastern Bering Sea (Shevlyakov and Parensky 2010). The paucity of information on adult trophic-phase Arctic and Pacific lampreys in the North Pacific Ocean warrants investigation for informing future hypotheses regarding native lamprey parasitism in this highly productive and economically valuable ecosystem.

My goal was to utilize lamprey wounds observed on a marine host to infer ecological interactions between native anadromous lampreys and host fishes in the North Pacific Ocean. I restricted my analyses to the eastern Bering Sea, where large-scale commercial fisheries occur and Arctic and Pacific lampreys are the only known species of parasitic lampreys present (Mecklenburg et al. 2002). I chose to examine Pacific Cod because this species is commonly captured in fishery surveys across a broad geographic expanse, often exhibit lamprey wounds, and are targeted in lucrative large-scale commercial fisheries. Before inferring ecological interactions, I needed to discern which lamprey species was inflicting wounds on Pacific Cod, so I examined similarities in the morphological shape of lamprey wounds and oral discs of Arctic and Pacific lampreys. To then see if wounding varied with host size, I explored relationships between lamprey wounding rates and Pacific Cod length. Finally, because I was interested in which characteristics of lamprey wounds were likely to reach a completely healed state as a means for inferring impacts to Pacific Cod survival, I explored lamprey wound severity and location on Pacific Cod across sequential stages of healing. Combined, this information provides an initial step towards describing and understanding the interactions of native lampreys and hosts in the eastern Bering Sea.

2.3 Methods

2.3.1 Data sources, processing, and classification

Pacific Cod were scanned for lamprey wounds during the International Pacific Halibut Commission (IPHC) annual longline surveys conducted from June through August in 2011 and 2012. This survey collected fishery-independent data on Pacific Halibut, with coverage from northern California to the eastern Bering Sea (Henry et al. 2013). The target sampling effort at a station was six skates with 100 baited hooks each, and for this study, a total of 250 stations in the eastern Bering Sea were sampled over two years. At each station, IPHC sea-samplers measured the total length of the first 15 Pacific Cod landed per skate and scanned them for potential lamprey wounds, such that the maximum number of Pacific Cod scanned per station was 90 fish. When lamprey wounds were suspected, IPHC sea-samplers took photographs orthogonal to the wounds using a Panasonic DMC-TS3, including information on the roughness of scales surrounding the wound, wound depression, and a length scale utilized in post-survey processing and analysis.

To describe the oral disc morphology of lampreys in the eastern Bering Sea, I opportunistically utilized lamprey specimens captured by the 2012 National Marine Fisheries Service (NMFS) benthic rope trawl survey. This survey was designed to collect biological and oceanographic data for assessing groundfish stocks and has occurred annually between June and August on the Bering Shelf since 1982 and biennially along on the Bering Slope and Aleutian Islands since 2002. Survey gear consisted of an 83-112 eastern otter trawl, with a 25.3-m headrope, 34.1-m footrope, 8.9- to 10.2-cm mesh net,

and 3.2-cm end mesh liner (Hoff 2013; Lauth and Nichol 2013). All specimens captured during this survey were identified as Pacific Lamprey based on their dentition, the most distinguishing character being three large supraoral lamina teeth (Mecklenburg et al. 2002). Counts of endolateral (2-3-3-2) and infraoral (5) teeth were also checked as slight variations in the number of these teeth can occur. These Pacific Lamprey specimens were predominantly captured near the continental slope (Figure 2.1).

Additional anadromous lampreys were opportunistically obtained from epipelagic trawls conducted during the 2012 Bering Aleutian Salmon International Survey (BASIS), which was designed to collect biological and oceanographic data to study the epipelagic ecosystem and has been conducted annually from August to early October in the eastern Bering Sea and Chukchi Sea since 2002. The survey gear consisted of a 198-m midwater rope trawl, with a 1.2-cm cod end mesh liner towed in the upper 50 m of the water column for approximately 30 minutes per station at speeds of 6.9–9.3 km/h (Farley et al. 2009). All specimens captured on this survey were identified as Arctic Lamprey based on their dentition, the most distinguishing character being two large supraoral lamina teeth (Mecklenburg et al. 2002). Counts of endolateral (2-2-2) and infraoral (6–10) teeth were also checked as slight variations to these teeth can occur. These Arctic Lamprey specimens were predominantly captured in the northeastern Bering Sea (Figure 2.1).

I digitally photographed oral discs of Arctic and Pacific lampreys, and measured disc dimensions using the image processing software ImageJ (Abràmoff et al. 2004). To photograph lamprey oral discs, I pressed them tooth-side down against a flat piece of glass so that the entire disc was visible, and images were taken facing upwards with a

Panasonic DMC-TS3. In ImageJ, I placed an elliptical perimeter around the exterior edge of the marginal teeth and inside of the oral fimbriae, recording the length of the major and minor axes making up the ellipse around the oral disc (Figure 2.2). An analysis of the correlation between lamprey size (total-length) and oral disc size (perimeter) was carried out for each species. I then used the aspect ratio, calculated by dividing the major axis by the minor axis, as a metric for comparing the morphological shape of oral discs. An oral disc would be a perfect circle at an aspect ratio of 1:1, and would become more oblong as the aspect ratio increased. An analysis of the correlation between lamprey size (total-length) and aspect ratio was used to test the assumption that oral disc aspect ratio did not vary by lamprey length.

I examined all photographs of suspected lamprey wounds taken by IPHC sea-samplers, and only further processed wounds that were assessed to be caused by a lamprey. Evidence that a wound was the result of a lamprey interaction included visible dentition patterns, circular or oval shape, evidence of a sliding oral disc, and scale loss on the surrounding skin (Lennon 1954; King 1980). In ImageJ, I placed an elliptical perimeter around the exterior edge of each lamprey wound and recorded the length of the major and minor axes of the ellipse (Figure 2.2). I then calculated the aspect ratio of each lamprey wound for comparison with the same measurements made on oral discs of Arctic and Pacific lampreys as described above. The margins of some lamprey wounds were not clearly discernible because of sloughing of the surrounding skin, so I categorized lamprey wounds with discernible margins as High Confidence and those without discernable margins as Low Confidence.

To examine interactions between anadromous lampreys and Pacific Cod, I classified lamprey wounds on Pacific Cod using methods adapted from lamprey studies in the Laurentian Great Lakes (King 1980). Similar methods have been utilized to research Pacific Lamprey interactions with various host species in the North Pacific Ocean (e.g., Orlov et al. 2009). In addition to morphological dimensions, I considered the following characteristics of lamprey wounds: degree of severity, degree of healing, and location on the Pacific Cod body. For individual Pacific Cod with multiple wounds from the same lamprey feeding event (as evidenced by sliding connections) only the most recent wound was counted to avoid inflating the perceived number of feeding lampreys (Ebener et al. 2006). When there was no connection, each wound was examined separately.

Each lamprey wound was first classified by severity. Wounds that penetrated into host muscle tissue and were associated with a depression were categorized as type A, whereas superficial wounds that did not penetrate into host muscle tissue or leave a depression were categorized as type B (Figure 2.3). Type-A wounds were inferred to result from a successful feeding event where blood and flesh were consumed. In contrast, type-B wounds were more likely the result of a failed attempt by a lamprey to feed or a successful blood feeding event only.

Four healing stages were used to classify lamprey wounds by the relative amount of time since a lamprey detachment (King 1980). Healing stages were characterized as follows: (1) rough skin surrounds the wound, no healing, and no re-pigmentation; (2) smooth skin surrounds the wound, limited healing evident, and no re-pigmentation; (3)

smooth skin surrounds the wound, considerable healing, and some re-pigmentation; and (4) complete healing of wound, complete re-pigmentation, and regeneration of scales (Figure 2.3). For this analysis, I defined "recent" wounds as those classified (type-stage) as A-1, A-2, and A-3 (Figure 2.3), following a convention set in lamprey research on the Laurentian Great Lakes (e.g., Prichard and Bence 2013). On the IPHC longline survey, lampreys were occasionally observed detaching during haulback, so I assumed that some stage-1 wounds were the result of premature lamprey detachment due to a fish being captured and brought to the surface. For wounds that had healed beyond stage 1, I assumed that lamprey detachment was most likely the result of lamprey satiation prior to the Pacific Cod being captured.

To examine patterns in locations of parasitism on Pacific Cod, lamprey wounds were assigned to body regions. I defined Pacific Cod body regions following Orlov et al. (2009): (I) anterior-dorsal, (II) posterior-dorsal, (III) anterior-ventral, (IV) posterior-ventral, (V) head, and (VI) caudal (Figure 2.4). For wounds that were connected via slide marks, I assigned the body region using the location of the wound with the most recent detachment, such that an A-1 wound in region II connected to a B-3 wound in region III would only be counted as a single A-1 wound in region II.

2.3.2 Comparison of oral discs and lamprey wounds

I compared differences in the aspect ratio among Arctic Lamprey oral discs, Pacific Lamprey oral discs, and recent lamprey wounds on Pacific Cod using an ANOVA test followed by a Tukey-Kramer test for multiple pairwise comparisons. Because samples were opportunistically collected, the sampling design was unbalanced, and

detection of possible heterogeneity among the variances necessitated the inclusion of a Welch's correction for the ANOVA test (Welch 1951) and use of the Dunnett modified Tukey-Kramer test (Dunnett 1980). I assumed that the oral disc aspect ratios calculated for each lamprey species were constant for individuals beyond the sampled length ranges. I further assumed that the aspect ratio of an oral disc was retained in lamprey wounds on Pacific Cod. To minimize unknown distortion effects in the shape of a wound that has completely healed, I limited this analysis to recent lamprey wounds. To minimize bias from measurement error, I only included lamprey wounds classified as High Confidence. Finally, I assumed independence of samples because the lamprey specimens were captured in different surveys than the Pacific Cod, and thus sampled lamprey were not likely to be responsible for wounds observed on sampled Pacific Cod.

2.3.3 Pacific Cod length and lamprey wounds

I investigated relationships between lamprey wounding rates and Pacific Cod length in two ways. First, I compared the number of Pacific Cod exhibiting at least one recent lamprey wound to the number of Pacific Cod exhibiting no lamprey wounds using length-based size-classes and a chi-square contingency table. I selected size classes using midpoints between mean length-at-age estimates for age-5, age-6, age-7, and age-8 Pacific Cod captured in the Bering Sea in 2011 resulting in four groups: <65 cm, 65–70 cm, 71–78 cm, and >78 cm (Thompson and Lauth 2012). In these comparisons, a single Pacific Cod could have multiple separate recent lamprey wounds, but was only counted once.

Second, I utilized a generalized additive modeling (GAM) framework to explore how the number of recent lamprey wounds related to Pacific Cod length (Hastie and Tibshirani 1990). Pacific Cod total length was only measured to the nearest centimeter, so counts of Pacific Cod scanned and recent lamprey wounds were organized by 1 length bins. The model was as follows:

$$Y \sim \beta_0 + s(n) + s(L) + \varepsilon,$$

where Y is the number of recent lamprey wounds, s(n) is the smooth function of the number of fish scanned for lamprey wounds, s(L) is the smooth function of the length of Pacific Cod, β_0 is the intercept, and ε is the error term. Because the response variable was counts of recent wounds, I initially investigated fitting the model with a Poisson distribution. However, the variance was greater than the mean, suggesting the Poisson distribution was over-dispersed. To remedy this, I assumed a negative binomial distribution allowing the variance to be a quadratic function of the mean with the addition of a scale parameter theta (Venables and Ripley 2002). Smooth functions for the number of fish scanned and the length were selected using performance iteration, selecting functions by generalized cross-validation and ensuring that the estimate of theta was as close to one as possible (Wood 2011). In this analysis, a single Pacific Cod exhibiting multiple recent lamprey wounds would contribute more than one count to the assigned length bin.

2.3.4 Classified lamprey wounds on Pacific Cod

To explore associations between lamprey wound severity (type A or B) and healing (stage 1–4), I used a chi-square contingency table. I assumed that type-B lamprey

wounds had little or no impact on Pacific Cod survival, so type B acts as a control group to which type A wounds can be compared. If type-A lamprey wounds had no effect on Pacific Cod survival beyond that of type-B wounds, I would expect the null hypothesis of no association between healing stage and wound type to be supported (i.e., the ratio of type-A: type-B lamprey wounds would be maintained across all healing stages).

To investigate associations between lamprey wound location on a Pacific Cod (regions I–VI) and healing (stages 1–4), I conducted a chi-square contingency test. I included only type-A lamprey wounds to remove any confounding effects introduced by differences between type-A and type-B wounds. If the location on a Pacific Cod where lamprey feeding occurred had no effect on the survival of the Pacific Cod, I would expect the null hypothesis of no association between healing stage and wound location to be supported (i.e., the proportion of lamprey wounds in each body region would remain constant across all healing stages). Because the expected values for some healing stage-body region combinations (1-I, 1-II, 3-I, 3-II, 4-I, 4-II, 4-IV, and 4-V) were low (<5), I approximated the P-value using a Monte Carlo simulation with 5,000 replicates (Hope 1968). Additionally, no type-A lamprey wounds were observed in region VI, so only regions I–V were included.

All statistical analyses were conducted using R version 2.12.2 (R Development Core Team 2011). The “mgcv” package was used for conducting generalized additive modeling (Wood 2011), and the “DTK” package was used to conduct multiple pairwise comparisons (Dunnett 1980). Statistical tests were evaluated at a significance level of $\alpha = 0.05$.

2.4 Results

2.4.1 Comparison of oral discs and lamprey wounds

I calculated the aspect ratio for 28 Arctic Lamprey oral discs, 46 Pacific Lamprey oral discs, and 148 recent lamprey wounds on Pacific Cod captured in the eastern Bering Sea (Figure 2.1). Arctic Lamprey specimens had total lengths of 27.2–43.9 cm with oral disc perimeters of 42.7–64.1 mm, and oral disc perimeter positively and significantly increased with lamprey length ($R^2 = 0.83$, $P < 0.001$, Figure 2.5). Pacific Lamprey specimens had total lengths of 47.2–71.3 cm with oral disc perimeters of 75.3–102.6 mm, and oral disc perimeter positively and significantly increased with lamprey length ($R^2 = 0.62$, $P < 0.001$, Figure 2.5). Recent lamprey wounds on Pacific Cod had perimeters ranging from 25.3–120.0 mm. Oral disc aspect ratio did not exhibit a significant trend with total length for Arctic Lamprey ($R^2 = 0.02$, $P = 0.40$) or Pacific Lamprey ($R^2 = 0.00$, $P = 0.81$), supporting the assumption that aspect ratio remains constant with length by lamprey species (Figure 2.5). Aspect ratio differed among Arctic Lamprey oral discs, Pacific Lamprey oral discs, and recent lamprey wounds on Pacific Cod ($F = 36.8$, $df = 2, 66$, $P < 0.001$). A Dunnett modified Tukey-Kramer pairwise comparison of aspect ratios indicated Arctic Lamprey oral discs were significantly more oblong than Pacific Lamprey oral discs ($P < 0.001$) and recent lamprey wounds found on Pacific Cod ($P < 0.001$), whereas the aspect ratio of Pacific Lamprey oral discs and recent lamprey wounds found on Pacific Cod were not significantly different in morphological shape ($P = 0.35$; Figure 2.6).

2.4.2 Pacific Cod length and lamprey wounds

In total, 8,746 Pacific Cod were scanned for lamprey wounds and 331 recent lamprey wounds were observed on 260 Pacific Cod. Of the four size classes of Pacific Cod, the lamprey wounding rate was lowest (2.0%) for Pacific Cod in the smallest size class (<65 cm) and greatest (3.5%) for Pacific Cod in the largest size class (>78 cm). The difference in wounding rate was greatest between the smallest two size classes, becoming progressively less between larger size classes. A rate of 2.97% recently wounded Pacific Cod was expected if there was no difference among size classes, but the lamprey wounding rate varied significantly among Pacific Cod size class ($\chi^2 = 14.7$, df = 3, P = 0.002), increasing with each consecutively larger size class of Pacific Cod (Figure 2.7). Although Pacific Cod with multiple lamprey wounds were not as common as those with a single wound, the proportion of wounded fish exhibiting multiple wounds also consistently increased with consecutively larger size classes, from 0.37% to 0.61%.

A GAM analysis revealed an increase in the number of recent lamprey wounds with an increase in Pacific Cod length and in the number of fish scanned per length bin. The scale parameter theta was 2.443, accommodating an increase in variance with the mean. The number of lamprey wounds significantly increased with the number of Pacific Cod scanned (P < 0.001), but a nonlinear relationship suggests that the most abundant size classes may reach wounding saturation (Figure 2.8). Specifically, Pacific Cod of intermediate lengths were scanned at much higher frequency than smaller and larger lengths, but after including an explanatory term to account for the varying number of fish scanned per length bin, the wounding rate increased from small- to intermediate-sized

fish, reaching an apparent asymptote at a length of approximately 78 cm ($P < 0.001$; Figure 2.8).

2.4.3 Classified lamprey wounds on Pacific Cod

Of the 8,746 Pacific Cod scanned for lamprey wounds, 365 were observed with one, 46 with two, 12 with three, and nine with more than three. For freshly inflicted stages 1 and 2, penetrating type-A wounds, A-1 (9.7%) and A-2 (43.2%), were more prevalent than superficial type-B wounds, B-1 (2.4%) and B-2 (13.4%), but for more healed stages 3 and 4, type-B wounds, B-3 (14.3%), and B-4 (5.9%), were more prevalent than type-A wounds, A-3 (8.7%) and A-4 (2.4%). The ratio of type-A:type-B wounds significantly varied with healing stage ($\chi^2 = 88.3$, df = 3, $P < 0.001$), shifting from type A being nearly four times as frequent in observed stage-1 lamprey wounds to type B being approximately twice as frequent in observed stage-4 lamprey wounds (Figure 2.9).

Of the 345 penetrating type-A lamprey wounds identified on Pacific Cod, the majority were observed in region III (54%), the anterior ventral portion of the fish, compared to regions I (9.6%), II (9.3%), IV (11.9%), and V (15.4%), and 15.1% were stage 1, 67.5% were stage 2, 13.6% were stage 3, and 3.8% were stage 4. The proportion of type-A lamprey wounds by location on the Pacific Cod body did not vary significantly among healing stages ($\chi^2 = 15.8$, df = NA, $P = 0.19$), remaining relatively constant across all four (Figure 2.10).

2.5 Discussion

The results from this study indicate that lamprey wounds observed on Pacific Cod in the eastern Bering Sea are most likely inflicted by Pacific Lamprey, and penetrating

lamprey wounds may have a negative impact on these hosts. Host size is an important factor to consider when investigating interactions with lampreys, and for Pacific Cod, larger individuals were significantly more likely to exhibit a recent lamprey wound compared to smaller conspecifics. Furthermore, lamprey parasitism that results in the penetration of muscle tissue is observed four times more frequently than superficial wounding, but the latter is twice as likely to be observed in a completely healed state as the former. Although type-A lamprey wounds were observed most frequently in the ventral and pectoral region of the Pacific Cod, no significant trends between wound location and healing stage were found.

The approach of using lamprey wound shape indicates that lamprey wounds on Pacific Cod were a similar circular shape to Pacific Lamprey oral discs, suggesting that parasitism on Pacific Cod is executed by Pacific Lampreys. Although Pacific Lampreys used in this study were all larger than collected Arctic Lampreys, both species can overlap in size (Orlov et al. 2008, 2014). As a result, wound size alone cannot be used for differentiating the inflicting species. Additional support for positing that wounds can be attributed to Pacific Lampreys comes from the observation of four lampreys that were landed attached to Pacific halibut during the IPHC longline survey in 2012 and, all four individuals were positively identified as Pacific Lampreys. Because aspect ratio results corroborate geographic distributions of lampreys (see Chapter 1), I believe that the majority, if not all, of lamprey wounds observed on Pacific Cod in the eastern Bering Sea can be confidently attributed to Pacific Lamprey. Therefore, further inferences of parasitic lamprey interactions with fish herein will be limited to this lamprey species.

The relationship between lamprey wounding rate and Pacific Cod length exhibited a logistic shape, which has been observed in other lamprey-host interactions. For example, Sea Lamprey wounding rates have been described as increasing with Lake Trout length before reaching an asymptote (Rutter and Bence 2003; Prichard and Bence 2013). Two alternative hypotheses may explain the logistic relationship between lamprey wounding rate and host length. The first hypothesis is size-selective parasitism of hosts by lampreys, which predicts that the largest available hosts would be selected for feeding (Farmer and Beamish 1973; Cochran 1985). This hypothesis aligns with optimal foraging theory (Emlen 1966; MacArthur and Pianka 1966), because large hosts would sustain longer feeding periods than smaller hosts and minimize additional energy expenditure associated with finding a new host. Evidence to support the size-selective hypothesis has been observed in laboratory investigations of Sea Lamprey (Swink 2003). In the Bering Sea, Pacific Cod shoal, thereby providing lampreys with the opportunity to select hosts based on size. Assuming that all the Pacific Cod captured from each station were equally available to a lamprey, the size-selective parasitism hypothesis would predict that at each station, the mean length of fish with a lamprey wound would exceed the mean length of unharmed fish. Although the mean length of a Pacific Cod exhibiting a lamprey wound was larger than the mean length of unharmed fish at two thirds of the stations, the opposite was true at the remaining one third, suggesting that smaller Pacific Cod are still parasitized when larger conspecifics are available.

An alternative hypothesis is size-dependent survival of hosts, which predicts that all sizes of hosts are parasitized but smaller hosts are less likely to survive compared to

larger conspecifics. This phenomenon has been observed in the parasitic relationship between Sea Lamprey and Lake Trout, Lake Sturgeon, Burbot, and Rainbow Trout (Farmer et al. 1975; Swink 2003; Patrick et al. 2009). The results in this study support the size-dependent survival hypothesis because all sizes of Pacific Cod were being parasitized, not just the larger individuals, yet there was a preponderance of wounds on larger Pacific Cod in the observed data, suggesting a larger fish was more likely to survive a lamprey feeding event and be observed in sampling than a smaller fish. A potential explanation for the asymptote observed at approximately 78 cm in length is that Pacific Cod larger than this length have attained a size beyond which size-dependence survival no longer occurs. It is also possible that a combination of size-selective parasitism and size-dependent survival of hosts is responsible for the relationship between lamprey wounding and Pacific Cod length observed.

Examination of lamprey wounds suggests that Pacific Cod experience lamprey-related mortality when muscle tissue is penetrated during parasitism. This assertion is supported by the fact that as wounds progressively healed, transitioning from stage 1 to 4, the number of penetrating type-A wounds consistently declined relative to superficial type-B wounds. If I conservatively estimate mortality of Pacific Cod related to type-B wounds to be zero, I can infer any departure from this baseline as an additional effect related to penetrating type-A wounds. Type-A wounds were observed four times as often as type-B wounds at a recently inflicted stage 1, but half as often at a completely healed stage 4. From this observation, I infer that Pacific Cod with a type-A wound are approximately four times less likely to reach a completely healed state compared to those

with a type-B wound. Although lamprey parasitism could directly cause a decrease in Pacific Cod survival, other possible reasons include increased susceptibility to predation or infection, or increased energy expenditure related to an open type-A wound. Although quantifiable estimates of lamprey-induced mortality cannot be made from this study because individual Pacific Cod were not resampled, the results herein do suggest that at the least, Pacific Lamprey parasitism may be related to a nominal portion of Pacific Cod mortality in the eastern Bering Sea.

The proportions of type-A wounds occurring in the five body regions examined for Pacific cod remained relatively constant for all four healing stages, providing no evidence that the location of a lamprey wound on a Pacific Cod impacted the survival of Pacific Cod. If lamprey parasitism directly had a negative impact on the survival of a host, this effect should be exacerbated when wounds are in vital regions III and IV, compared to non-vital regions I, II, and IV (Figure 2.4). However, because lamprey wounds in all vital and non-vital Pacific Cod body regions appeared equally likely to reach a completely healed state, I believe that direct mortality from lamprey feeding is unlikely in the examined lamprey-host interaction.

A preponderance of lamprey wounds observed on Pacific Cod occurred in body region III, the anterior ventral portion of the fish, which is consistent with a previous study of Pacific Lamprey wounds on Pink and Chum salmon in the western Bering Sea (Shevlyakov and Parensky 2010). The reason for lampreys attaching to the anterior ventral portion of a host is not investigated herein, but one possible hypothesis is the relatively high blood flow at this vital region. This phenomenon has been widely reported

for Sea Lamprey parasitism on a variety of hosts, and is generally attributed to low water flows, thin muscle layers, and fewer scales in this region (Farmer 1980; Cochran 1986; Cochran and Lyons 2010; Nichols and Tscherter 2011). These factors are likely to influence where Pacific Lampreys attach to Pacific Cod.

Although this study did not investigate differences between direct and indirect mortality resulting from lamprey parasitism, inferences can be made by combining severity and body-region results. I hypothesize that the majority of lamprey-related mortality of Pacific Cod is caused by indirect effects of lamprey parasitism because if direct effects from a lamprey feeding event were the main cause, I would expect wounds in vital body regions (e.g., the head) to result in increased mortality relative to wounds in non-vital body regions (e.g., dorsal muscle tissue). Inferring that reduced survival of Pacific Cod is associated with type-A wounds, but feeding in vital regions is not, I believe that Pacific Cod are more susceptible to indirect causes of mortality related to lamprey parasitism such as secondary infections or predation than they are to direct mortality resulting from lamprey parasitism itself.

The opportunistic sampling utilized in this study introduced some challenges that should be mentioned. First, Pacific Cod examined in this study were limited to the continental slope region, which is a region where Pacific Lampreys are found but Arctic Lampreys are not (Orlov et al. 2008, 2014). As a result, lamprey wounding on Pacific Cod was not formally quantified herein for regions where Arctic Lampreys are abundant. However, the 2011 and 2012 NMFS benthic trawl surveys that occurred across the eastern Bering Sea continental shelf and slope does provide qualitative information on

lamprey wounds observed on Pacific Cod. The incidence of lamprey wounds on the Pacific Cod that were examined was very low across the Bering Shelf (<10 lamprey wounds in a year), suggesting that Pacific Cod in this region do not frequently interact with Arctic Lampreys that are found in this region.

The inclusion of a multiple host species representing a variety of body sizes and the additional collection of health parameters such as gonado-somatic indices and blood chemistry parameters can improve our understanding of the relative health impacts lamprey parasitism causes to individual host fish and their populations (Pelenev et al. 2008; Pelenev et al. 2010; Sepulveda et al. 2012). Combining this type of field research with laboratory studies will be beneficial towards understanding preferences that lampreys exhibit when searching for hosts, as well as the potential impacts lampreys can have on individual hosts and populations. In addition, wounding rates could be incorporated into already occurring fisheries surveys as an additional means of monitoring trends in lamprey abundance in this region, though additional investigation into the relationships between lampreys and hosts will aid in the interpretation of this type of information. For example, it is unclear if a relative increase in lamprey abundance would be reflected in wounding rates, or if lamprey abundance is actually a function of host availability as suggested by Murauskas et al. (2013), which would result in a more consistent annual wounding rate. Multi-year investigations will be necessary to begin answering these types of questions.

This study takes an initial step towards understanding native lamprey-host interactions in the eastern Bering Sea, which has previously not been examined. Lamprey

parasitism is a potential source of mortality to a variety of fishes in the eastern Bering Sea, and the size-dependent impacts of lampreys on different hosts should be further investigated to assess the potential for negative impacts to fisheries. In addition to freshwater threats to lampreys, variations in lamprey abundance may be related to the availability of hosts in the ocean (Lança et al. 2013; Murauskas et al. 2013), and this issue represents an ecosystem-based management concern not currently included in any marine fisheries management plans. Further investigation into the interactions of anadromous lampreys and host fishes in this region will increase our understanding of this important feeding period, thereby allowing for better informed management and conservation measures for lampreys and their hosts in the future.

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2.8 Figures

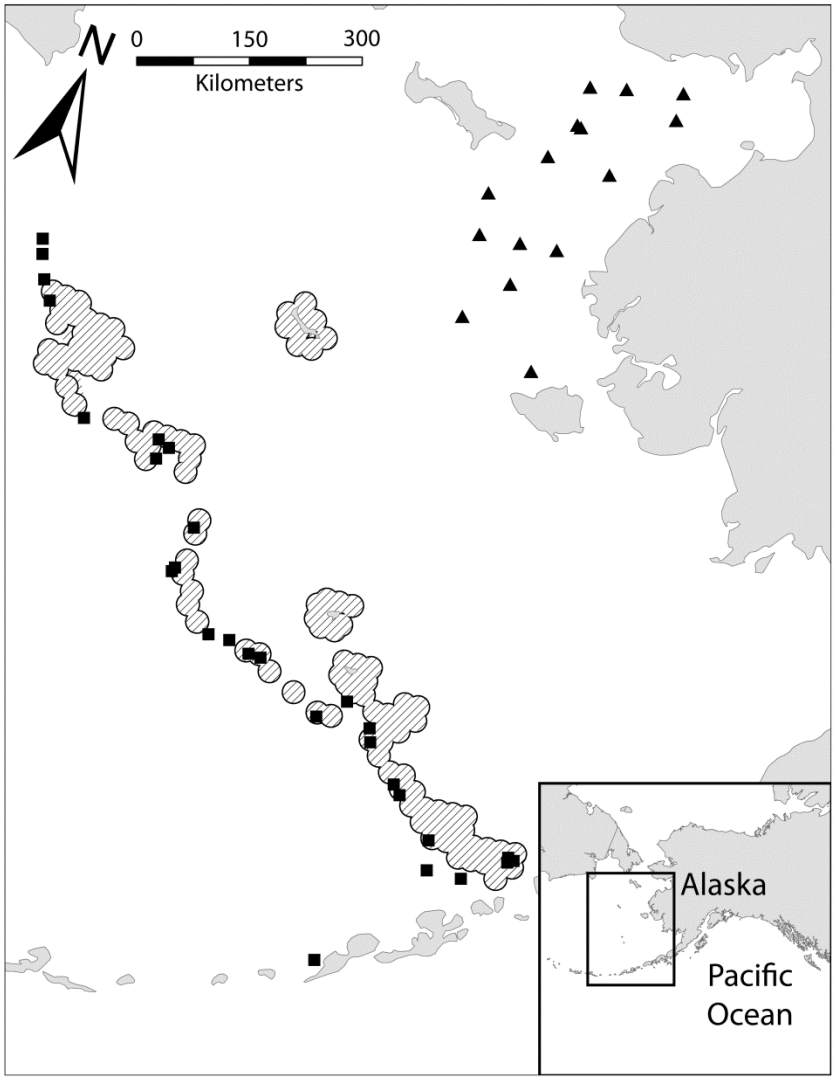

Figure 2.1. Map of the study region in the eastern Bering Sea (map extent indicated by rectangle on the lower right inset), displaying trawl stations where Arctic Lamprey (black triangles) and Pacific Lamprey (black squares) were collected in 2012 and longline stations where Pacific Cod were captured and scanned for lamprey wounds in 2011 and 2012 (diagonal lines indicate a 15-km buffer around stations for display purposes).

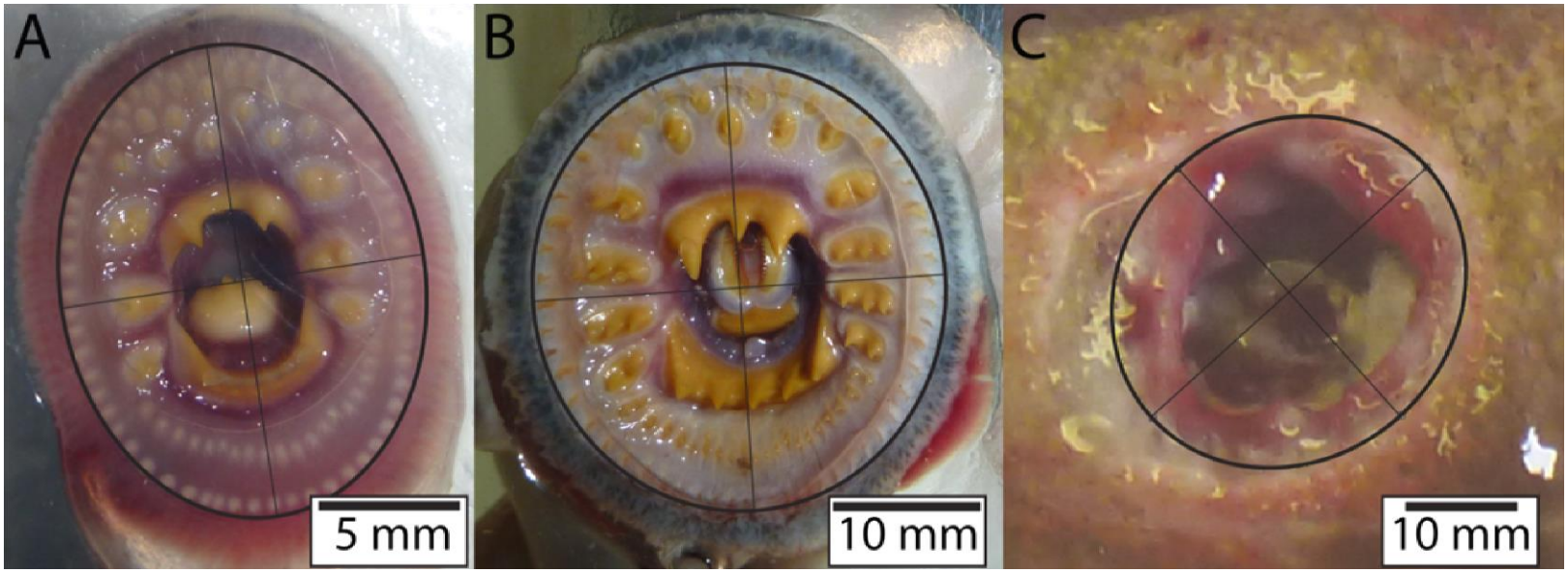

Figure 2.2. Examples of aspect ratio measurements for A) an Arctic Lamprey oral disc, B) a Pacific Lamprey oral disc, and C) a lamprey wound on a Pacific Cod.

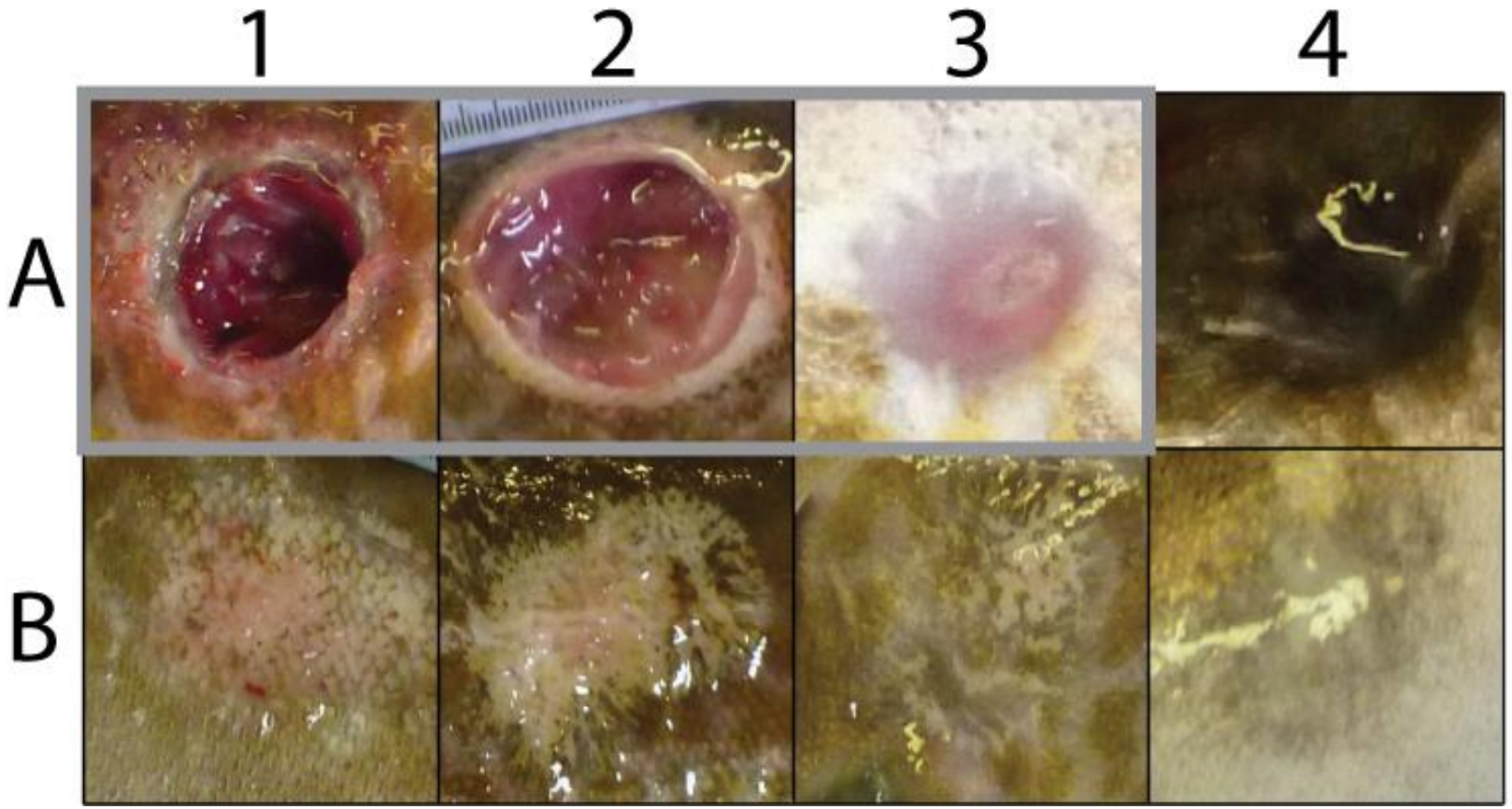

Figure 2.3. Examples of type-A and type-B lamprey wounds on Pacific Cod illustrating progressively healed stages 1 to 4 (left to right). Gray box indicates lamprey wounds that are referred to as “recent” in this study.

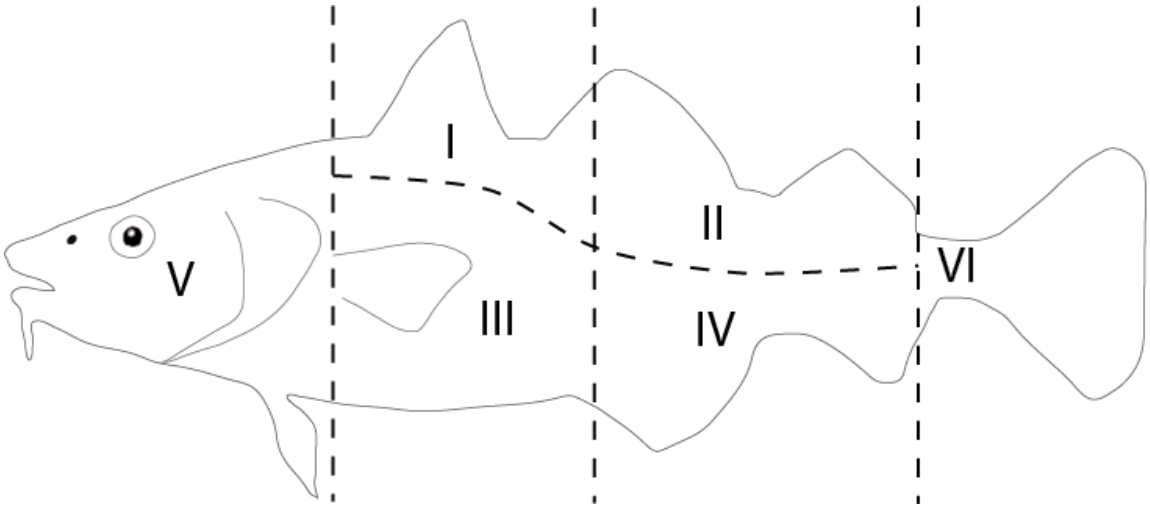

Figure 2.4. Pacific Cod body regions used to classify the locations of lamprey wounds. (Adapted from Orlov et al. 2009)

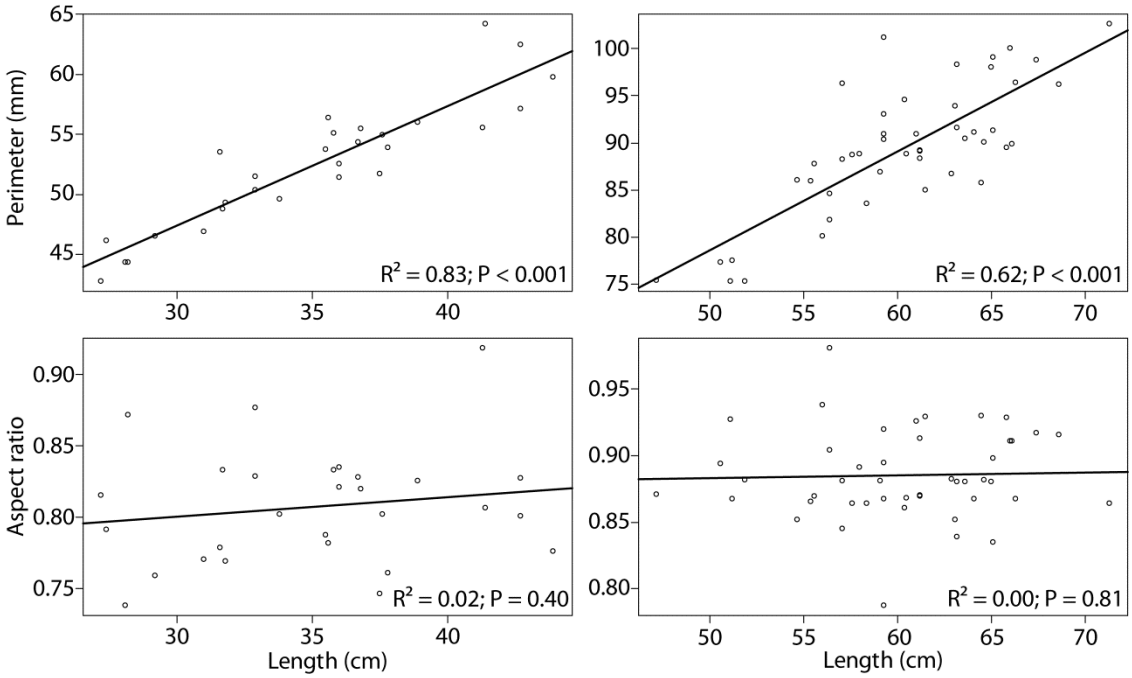

Figure 2.5. Correlations between lamprey length and oral disc measurements, showing perimeter (top) and aspect ratio (bottom) for Arctic Lamprey (left) and Pacific Lamprey (right). R-squared and p-values are shown in the lower right of each panel.

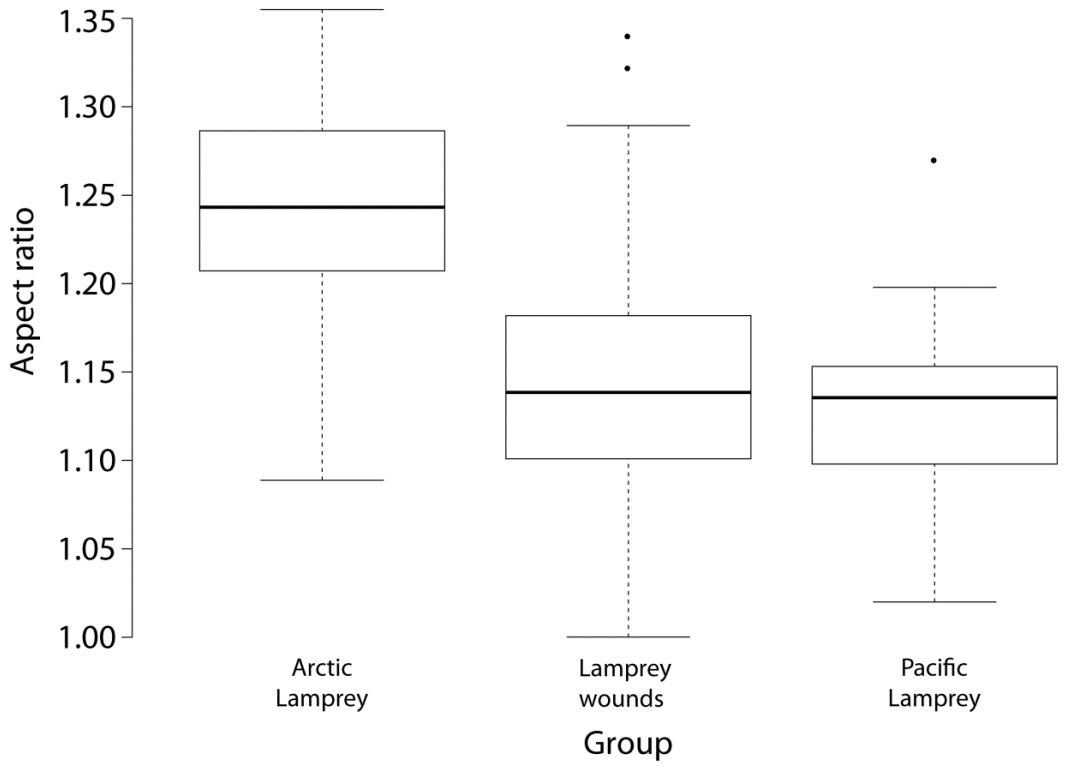

Figure 2.6. Box-and-whisker plot of lamprey oral disc and wound aspect ratios. For each group, the median is shown as the bold horizontal black line, the hinges of the box mark the first and third quartile, the whiskers designate a 1.5 interquartile range, and solid black circles indicate outliers.

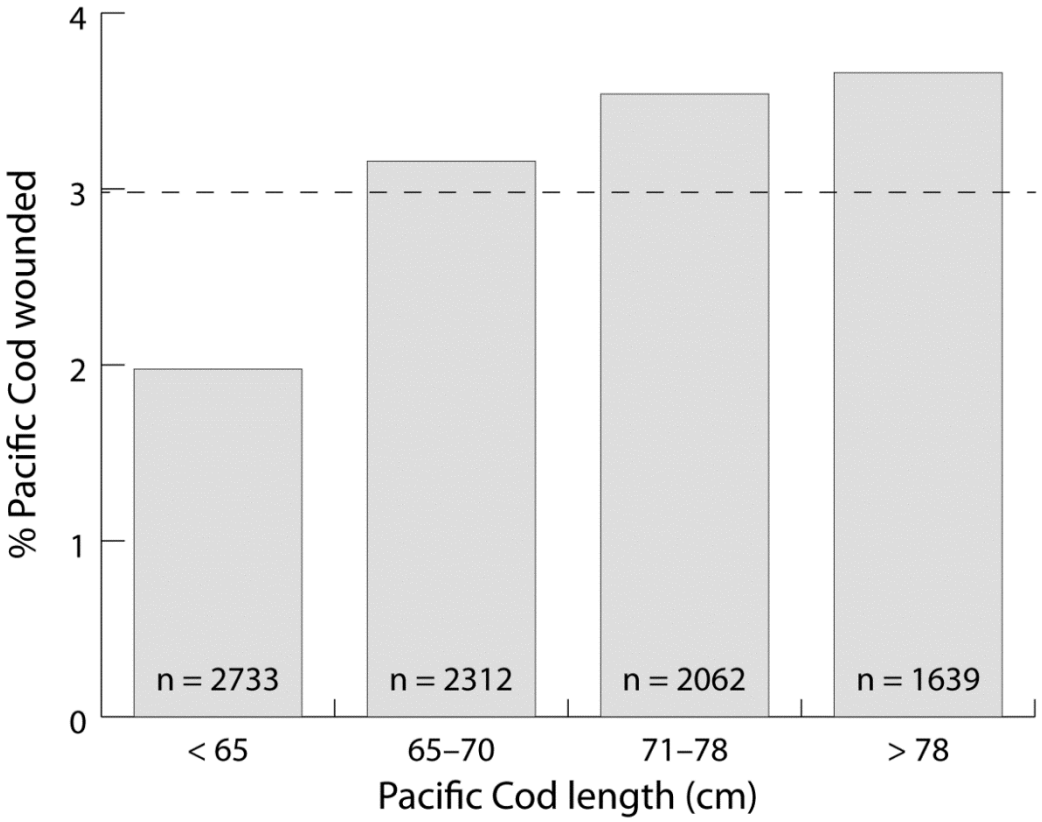

Figure 2.7. Percent of Pacific Cod exhibiting recent lamprey wounds for four length-based size-classes. Dashed line indicates the expected wounding rate from a chi-squared distribution.

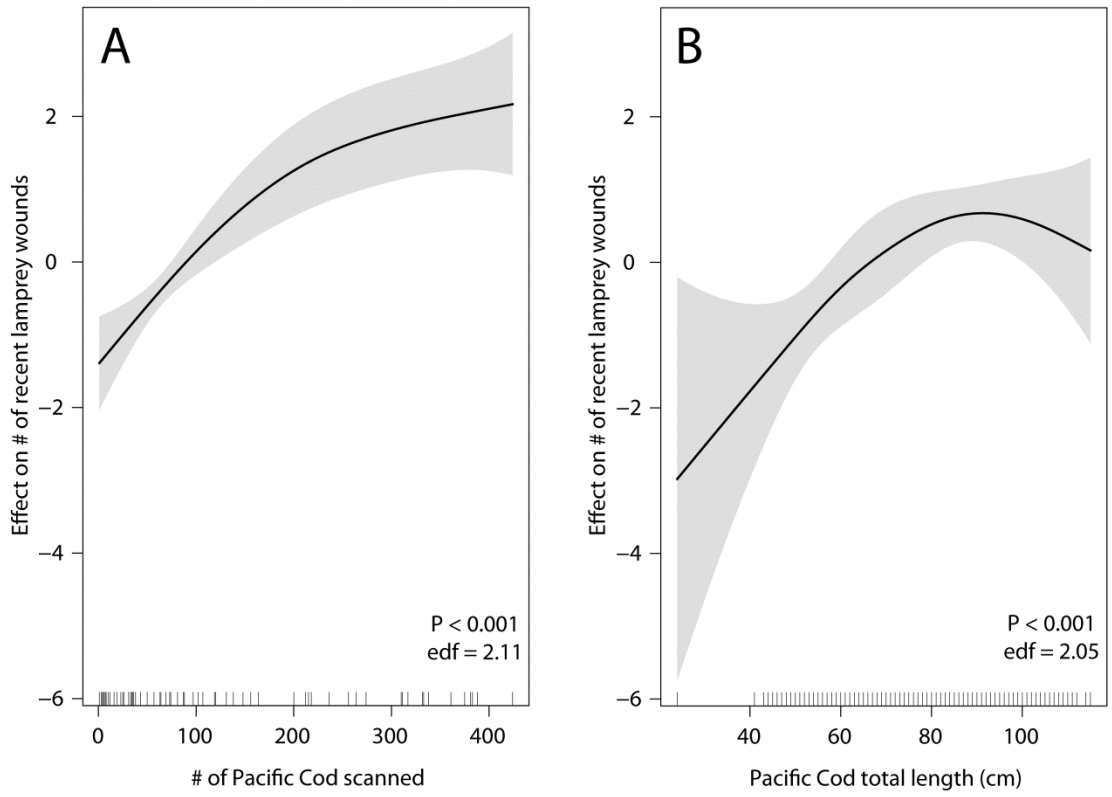

Figure 2.8. Generalized additive model (GAM) partial regression plots of wounds from lampreys exhibited on Pacific Cod. Smooth functions of A) the number of Pacific Cod scanned per length bin and B) the length of Pacific Cod are shown. Hash marks on x-axis indicate samples, and shaded regions indicate 95% confidence intervals. P-values based on chi-square test and estimated degrees of freedom (edf) are shown in the lower right.

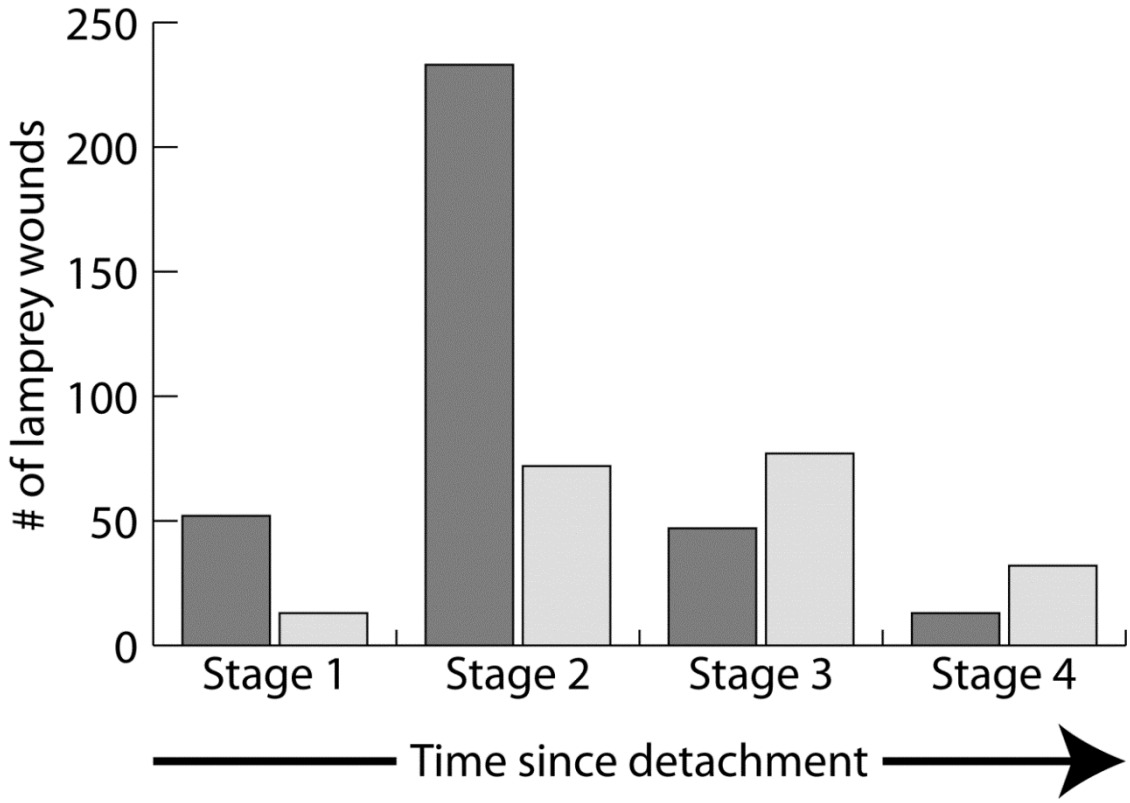

Figure 2.9. Frequency of lamprey wounds across four sequential healing stages, where penetrating type-A wounds are shown in dark gray and superficial type-B wounds are shown in light gray.

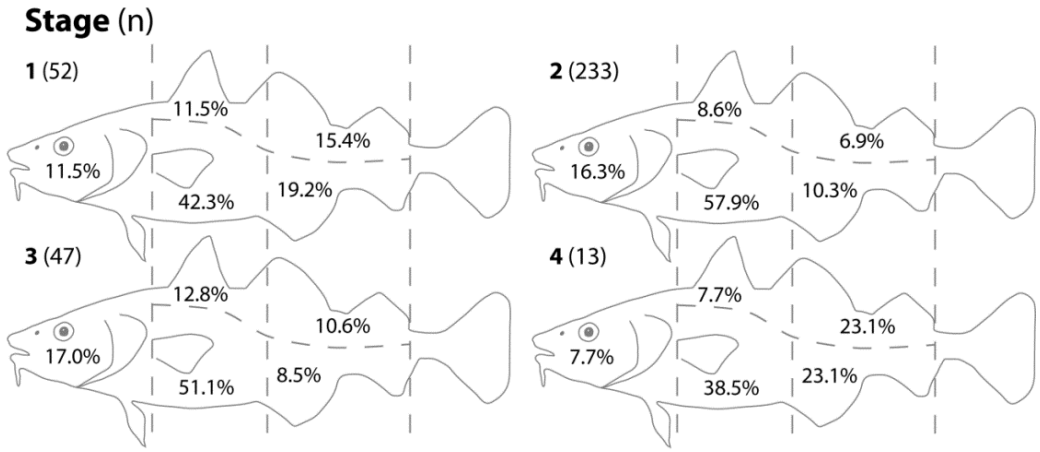

Figure 2.10. Locations and frequency of penetrating type-A lamprey wounds on Pacific Cod shown across four healing stages, a gradient in which stage 1 is most recently inflicted and stage 4 is completely healed.

General Conclusion

Lampreys represent an evolutionary success, and biologists and resource managers should take necessary steps to ensure the continued existence of this ecologically important group of organisms. Parasitic, anadromous lampreys have additional economic and cultural value, making these species particularly important to those cultures that harvest them. However, the period spent feeding in the ocean that unites anadromous lampreys, has largely been ignored by researchers. I have shown that opportunistically captured lampreys in the ocean provide a way to explore anadromous lamprey ecology and allow researchers to generate hypotheses for future directed studies. I found evidence that anadromous lampreys are distributed along geographically distinct areas in the eastern Bering Sea, and associations with different potential host fish is one possible reason for this observation. I also found that Pacific Lamprey native to the North Pacific Ocean may have a potentially negative impact on Pacific Cod that are parasitized, with host size being an important factor to consider. These results provide a starting point by which future research can reveal the nature of lamprey-host relationships in the North Pacific Ocean, and as the National Marine Fisheries Service progresses towards an ecosystem-based approach to fisheries management, consideration of lamprey-host interactions may become of greater concern to marine resource managers.

There is great potential to continue research on the lampreys in the North Pacific Ocean, especially in the ocean, and many of these opportunities would only require minor additions to already occurring fishery monitoring programs. In Alaska, additional research on lampreys at all stages is necessary to provide information for conservation

and management of the resource (ADFG 2006), and lamprey information could be incorporated into existing stream and river surveys. In the ocean, the National Marine Fisheries Service Observer Program currently documents lampreys (AFSC 2013), but species identification is rare and could easily be improved by including dentition in observer training manuals. Furthermore, recording lamprey wounds on fish captured during marine surveys may aid in understanding which species and locations are important for lamprey feeding.

An improved understanding of oceanic ecology of lampreys may couple with freshwater sampling that is already occurring to improve our understanding of lamprey dynamics. For example, the Arctic Lamprey fishery on the Yukon River is annually sampled during the spawning run (L. DuBois, Alaska Department of Fish and Game, personal communication), which should be investigated for biological and ecological correlations that link samples of this species collected in the Bering Sea. Variations in the number, size, and condition of lampreys is variable in annual collections of lampreys from marine and freshwater surveys, and potential links between these variations as well as causes occurring at both freshwater and marine phases are likely. Additionally, there is no current forecasting of spawning run strength, which can make management difficult, especially during times of depressed run strength. However, host availability in the ocean was correlated with the number of spawning-phase Pacific Lamprey entering the Columbia River (Murauskas et al. 2013), not only providing a potential metric for predicting spawning run strength but also linking the marine and freshwater life-history

stages of this species. This holistic type of approach will provide a more comprehensive understanding of lamprey population dynamics.

An increased understanding of the ecology of lampreys will have implications on human social systems in which lampreys play an important role. Athabaskan Alaskan Natives and members of Pacific Northwest Tribes, including Nez Perce, Umatilla, Yakama, Warm Springs, Yurok, and Karuk, have a long history of fishing for lampreys in North American rivers (Close et al. 2002; Brown et al. 2005; Petersen 2009). The development of commercial lamprey fisheries is currently occurring in western Alaska (Bue et al. 2011), and the hosts that lamprey feed on in the ocean are also commercially exploited (Murauskas et al 2013). As we begin to identify important regions utilized by lampreys in the ocean, we can begin to understand how environmental stressors in these regions may influence lamprey populations, informing future lamprey conservation and management efforts. In addition, the impact of lamprey parasitism on commercially important species in the eastern Bering Sea is not well understood, and identifying areas for potential interactions between lampreys and commercially important species is the first step towards addressing this potential conflict.

Many hosts of anadromous lampreys are targeted by commercial fisheries, and lamprey-induced mortality can be viewed as a threat to commercial fish resources (Orlov et al. 2008, 2014). In the current state of affairs, commercial fishermen in the USA do not view lamprey parasitism as a great source of mortality to their targeted species, nor do they view the value lost due to lamprey wounds as significant (Q. Fong, University of Alaska Fairbanks, personal communication). As such, they do not pay much attention to

lamprey presence or parasitism beyond the novelty of these curious organisms. However, if we do not know the impacts lamprey parasitism has on commercial fish stocks, we should not ignore this potential interaction altogether as is the status quo.

Additionally, reductions in the abundance of marine fishes by commercial fisheries diminish the number of hosts available to adult trophic-phase lampreys, and this may cause declines in lamprey populations (Murauskas et al. 2013). However, research has been focused on freshwater problems and solutions related to lamprey declines, largely ignoring the adult trophic phase. Many of these freshwater issues are being addressed, such as the inclusion of lamprey friendly fish passageways (Moser et al. 2011) and transporting of spawning adults upriver of dams (Ward et al. 2012). These efforts may increase the number of adult lampreys spawning, but if a bottleneck during the adult trophic phase is hindering lamprey survival during this period, these efforts will be limited in their utility to ultimately restore lamprey populations. It is important to continue making efforts such as these as they can only benefit lamprey populations; however, if we can elucidate the importance of the adult trophic phase, we can better understand how all stages of the anadromous lamprey life cycle influence the overall success of a population. For example, the number of spawning-phase anadromous lampreys is likely a cumulative function of all previous life stages, the last of which is the adult trophic phase.

The lack of dialogue between marine resource users and freshwater lamprey fishermen precludes acknowledgement of the potential conflict between these user groups. Yet there is great potential for federal, state, and tribal agencies to work with

marine resource users towards understanding the importance of the adult trophic phase to overall lamprey population health and work together to alleviate unnecessary pressures. For example, noting where lampreys are captured and with which fishes they are found will provide information on important locations and species for lamprey feeding. In turn, efforts can be made to target these species outside of important lamprey feeding periods, allowing increased availability of hosts when they are most needed for lampreys. Typical stock assessments of marine fisheries are drafted for single species, but in Alaska, ecosystem impacts are also addressed. To date, depletion of the lamprey prey base via commercial fishing is undoubtedly an ecosystem impact that is not currently acknowledged.

Balancing the needs of different user groups is a constant task of resource managers, and lampreys are no exception. As lamprey restoration programs seek to restore anadromous lamprey populations in need, they should consider those marine resources that are needed to support their goals. Likewise, successes in lamprey restoration may be met with adverse reactions by commercial fishermen that experience increases in parasitism. One proactive step that can be made is opening a dialogue between these groups, allowing a better understanding of the impacts of lampreys and their hosts have on one another. The findings of this study provide valuable first insights into lamprey-host interactions in the Bering Sea and hopefully will serve as a catalyst for future research on this topic. As we begin to understand these complex interactions between anadromous lampreys and their hosts, we can incorporate marine life-history

into informed management and conservation decisions ensuring harvests of Arctic and Pacific lampreys for generations to come.

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